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Allan D. Cruickshank

Solitary Vireo

ADAPTIVE VARIATION IN THE GENUS *VIREO*

BY TERRELL H. HAMILTON

One aspect of a recently completed study (Hamilton, 1958MS) of species relationships in the genus *Vireo* was an analysis of intraspecific variation of certain external characters. The objective of this paper is to present the patterns of variation exhibited by those members of this genus having wide distributions in North and Middle America, and to comment on some possible explanations for the adaptive meanings of such patterns. A secondary purpose is an examination of the possibility that interspecific competition has been operative in furthering the ecological separation of two closely related, sympatric species, the Solitary and Yellow-throated vireos (*V. solitarius* and *V. flavifrons*).

There is an important need for more studies of intraspecific variation in several species of an avian genus rather than in single species alone; we need to know the extent and degree of conformity to ecogeographical rules in species of various genera in order to obtain a valid concept of the phenomena of parallel evolution and adaptation in response to environmental gradients. To reach this understanding, more comparative studies of variation within groups having both similar and different distributional patterns will be needed. Snow's (1954*a*; 1954*b*) analysis of variation in external morphology and habitat preferences within the species of *Parus* has shown how much information concerning the process of adaptation may be gained from such a comparative study. There are few other adequate studies of variation within avian genera, exceptions being the examinations by Miller (1941) and Pitelka (1951) of the genera *Junco* and *Aphelocoma*.

All too often, studies of character variation in relation to change in environment have stressed examples in agreement with the standard ecogeographical rules, and have failed to examine the exceptions which, as Mayr (1956:106) has recently emphasized, should receive more attention. Concerning this point, Salomonsen's (1955) study of migration and variation in some Old World species that previously were thought to represent inexplicable reversals of Bergmann's rule, and Moreau's (1957) analysis of climatic variation in the African populations of the *Zosterops* complex are two examples of studies that have demonstrated patterns of adaptations under different climatic or ecological conditions. Such studies provide convincing evidence of an adaptive significance for intraspecific variation.

Throughout this study, I have tried, where appropriate, to compare the genus *Vireo* with another continental, oscine genus, *Parus*, whose ecological and climatic adaptations in the Palearctic have been studied. There are, however, several basic differences in the general ecology of the species of

these two genera that do not permit the assumption of common mechanisms of adaptation applicable to both. Most species of *Vireo* (excluding endemic, insular forms in the Caribbean) are migratory or partially migratory and have discontinuous distributions in both temperate and tropical regions of the New World; as many as five species may be sympatric (although separated by habitats) during the breeding season, yet co-occupancy of the same habitat is almost unknown. The Old World members of *Parus* are resident or partially migratory species having continuous or discontinuous distributions primarily in the temperate regions of the Palearctic. In this group, co-occupancy of the same habitat appears well developed among the sympatric species during the breeding season; Snow (1954*a*:19) states that four or five species may occur together within the same habitat. Thus, with different ecological and ethological environments, dissimilar patterns of variation are not unexpected for the two genera.

In general for the species of *Vireo*, most of the characters studied showed clinal variation, but not necessarily in accordance with the accepted climatic or ecogeographical rules. Variation in body size (as indicated by wing length), bill length and tail length were exceptions. Bergmann's rule—that within one species individual body size tends to be larger in colder regions than in warmer regions—was found unsatisfactory for explanation of the variation patterns of the members of the genus. For example, in the Solitary Vireo (*V. solitarius*) the northern populations are migratory (Fig. 1) and have their winter quarters in Middle America (north to central Mexico), a region where resident or partially migratory populations may have either larger *or* smaller wing lengths than their northern counterparts.

Before continuing, I would like to point out that my conclusions, reported in this paper, on the adaptive significance of variation in body size within the species of *Vireo* and some other New World species *do not invalidate* Bergmann's rule. Rather, I interpret my findings to represent alternative possibilities: First, other selective forces (e.g., selective action of certain attributes of the summer environment—high temperatures and/or various humidities) may mask, modify, or interact with the selective action of cold temperature. Second, the winter temperatures to which the various populations of the species concerned are exposed may be above the "threshold" below which cold temperature would exercise a selective action. This second alternative would also permit the action or concurrent actions of other selective forces.

Methods

Wing length measurements were taken (to nearest 1.0 mm.) from wrist to tip of longest primary with wing flattened. Bill length (culmen) was measured from the nasal-frontal hinge with calipers (to nearest 0.5 mm.). Tail lengths were taken with calipers

measuring (to nearest 0.5 mm.) the distance from the base of the middle rectrices to their distal tips. Measurements from specimens showing worn or damaged feather tips were not included in the variation data presented in this paper. In determining the "breeding population samples" from which the measurements were taken, I tried to secure 10 or more male specimens collected during or immediately prior to the breeding

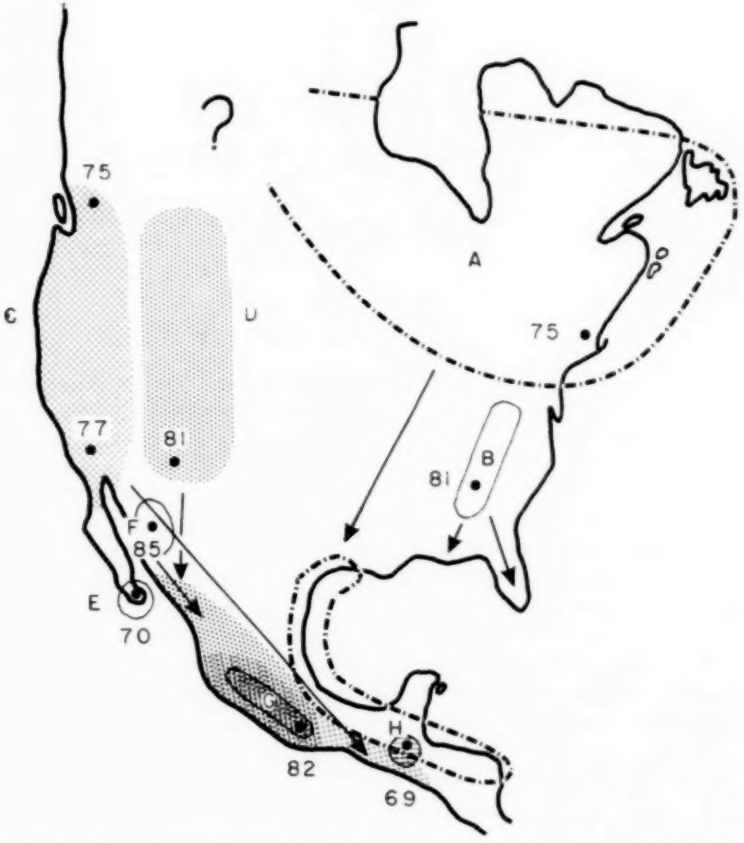

FIG. 1. Geographic variation in wing length within *Vireo solitarius* showing the breeding and wintering quarters of the various segments or populations. Arrows lead from breeding to wintering quarters; areas without arrows represent resident segments or populations. Black dots indicate geographic locations of breeding populations with mean wing lengths given to nearest 1.0 mm. (see Table 2). Segments: A, *solitarius*; B, *alticola*; C, *cassinii*; D, *plumbeus*; E, *lucasanus*; F, *pinicolus*; G, *repetens*; and H, *montanus*.

season in or about the same locality or region. Because of a slight sex difference in size, only male specimens were included. Measurements of differences between lengths of primary feathers (utilized in determining the "wing-tip index" values presented in Table 6) were taken to the nearest 1.0 mm.

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Species Groups within the Genus

Vireos are nine- or ten-primaried oscines which glean insects from foliage. The genus is restricted to temperate and tropical America with nearly all of the species occurring in North and Middle America. There are no species endemic to South America, although members of wide-ranging, polytypic species or superspecies occur there. Endemic and divergent representatives are found in the Greater Antilles. Members of the genus show virtually no evidence of sexual dimorphism in color. At least for the breeding season, monogamous pair formation is characteristic for all species. The habitat for the genus is primarily broadleaved vegetation, but the various species may be designated as being either thicket foragers or arboreal foragers.

The various species or superspecies may be divided (Hamilton, 1958MS) into the following species groups based on morphological and ecological characters:

Subgenus *Vireo*
(eye-rings and wing-bars present)

griseus group
(thicket foragers)

Species	*Breeding distribution*
V. griseus. White-eyed Vireo. (includes *V. pallens*, *V. crassirostris*, *V. gundlachii*, *V. modestus*, and *V. caribaeus*.)	Eastern United States, both coastal lowlands of Middle America, Bermuda, and various islands of the West Indies.
V. carmioli. Yellow-winged Vireo.	Mountains of Costa Rica and western Panama.
V. bairdi. Cozumel Vireo.	Cozumel Island off Quintana Roo.

V. osburni. Osburn's Vireo.	Blue Mountains of Jamaica.
V. nanus. Lawrence's Vireo.	Hispaniola and Gonave Island.
V. latimeri. Latimer's Vireo.	Puerto Rico.
V. bellii. Bell's Vireo.	Lowlands of southwestern United States, east to Mississippi Valley, and south to northern Mexico.
V. vicinior. Gray Vireo.	Arid lowlands of southwestern United States and northern Mexico.
V. nelsoni. Dwarf Vireo.	Southwestern Mexico (Michoacan, Guanajuato, and Oaxaca).

solitarius group
(arboreal foragers)

V. solitarius. Solitary Vireo.	Forested North America south through montane Mexico to highlands of Honduras.
V. flavifrons. Yellow-throated Vireo.	Broadleaved forests of eastern North America.
V. atricapillus. Black-capped Vireo.	Southwestern Kansas south through Oklahoma and west-central Texas to central Coahuila.
V. huttoni. Hutton's Vireo.	Southwestern British Columbia south through western United States (east to the Rocky Mountains and western Texas) to Mexico and Guatemala.

Subgenus *Vireosylva*
(eye-rings and wing-bars absent)

gilvus group
(arboreal foragers)

V. gilvus. Warbling Vireo. (includes *V. leucophrys.*)	Broadleaved forests (montane) of North, Middle, and South America.
V. philadelphicus. Philadelphia Vireo.	Eastern North America.

olivaceus group
(arboreal foragers)

V. olivaceus. Red-eyed Vireo. (includes *V. flavoviridis* and South American forms.)	Broadleaved forests (lowlands) of North, Middle, and South America; absent from southwestern United States and western Mexico.
V. altiloquus. Black-whiskered Vireo. (includes *V. magister.*)	Florida Keys and islands of the Caribbean (includes several coastal areas and islands of Yucatan, Quintana Roo, British Honduras, and Honduras).
V. hypochryseus. Golden Vireo.	Lowlands and foothills of western and southwestern Mexico.

Of these species, *V. griseus, V. solitarius, V. huttoni, V. gilvus,* and *V. olivaceus* are of wide distribution and demonstrate pronounced geographic variation. The remaining species of *Vireo* are either monotypic or polytypic species with relatively restricted distributions, and exhibit little or no ecogeographical variation.

Compared to presumably related oscine genera (e.g., the "coerebid" complex of honeycreepers or the *Dendroica* group of wood-warblers), the species of *Vireo* show little divergence in terms of habitat preferences, coloration, or modifications of the external morphology. With exception of two specialized species (*V. osburni* and *V. nanus*) endemic to islands in the Caribbean, the vireos appear to have uniform bill structures and essentially similar feeding adaptations.

The vireos are all fairly similar in appearance, being mostly yellow-greenish species characterized by the presence or absence of eye-rings, eye-stripes, and wing-bars. These are some of the morphological characters that taxonomists have used to determine the species and their relations to each other. The adaptive values of these characters are not clear, but presumably they may represent species recognition characters aiding individuals in finding conspecific mates. If this is true, a larger array of differences in such characters (ethological isolating mechanisms) might be expected when sympatric species exist in close proximity to one another; this might be especially important if the breeding and foraging positions of the different species overlap within a common habitat during the breeding season. Theoretically, there would be available, in different genera or groups of related species, alternative possibilities or "avenues" for obtaining (in response to natural selection) ecological and ethological compatibility for sympatric relationships.

In this respect, it is interesting to compare the habitat distributions of the species of *Parus* that are sympatric in the Old World with those of the sympatric species of *Vireo*, since both groups consist of insect-feeding species which forage in foliage. For sympatric species of *Parus* in the western Palearctic, *habitat co-occupancy* (sympatric species occurring together within the same habitat during the breeding season) is well developed, with the species concerned having different—but overlapping—feeding niches (see Gibb, 1954), having different coloration patterns, and belonging to different species groups or subgenera (as delimited by Snow, 1954*b*:566–567). However, morphologically similar species, such as the Willow Tit (*P. montanus*) and the Marsh Tit (*P. palustris*), both members of the *Poecile* species group, when sympatric in Europe normally are separated by habitat (Snow, 1954*b*: 579). In the Balkans (Serbia), a third member of the *Poecile* species group, the Somber Tit (*P. lugubris*) occurs in sympatry with these two species; all three related species are markedly separated from one another by their restriction to different habitats (Matvejev, 1950:177–180). Consequently, it would appear that differences in species recognition characters of the external morphology of some species (e.g., *P. major*, *P. caeruleus*, *P. ater*; each belonging to a different species group or subgenus) are associated in some unknown manner with the development of habitat co-occupancy as a type of

sympatric relationship. For species of *Parus* that have been studied, Hinde (1952:190) concludes that there are "few essential differences" in behavior between different species. Thus, for members of this genus occupying the same habitat, it would seem that selection has favored (along with the necessary adjustments in feeding ecology) traits of behavior which promote disregard of nonconspecific individuals.

In contrast to the general pattern for *Parus* cited above, the sympatric species of *Vireo* show *habitat separation* (sympatric species occurring during the breeding season in different or separate habitats or in different, stratal subdivisions of a habitat), somewhat similar to that of the members of the *Poecile* species group of *Parus*. Habitat separation for sympatric species of *Vireo* may be of two types: First, utilization of distinct habitats ("spatial separation") with no lateral overlap except for limited possibilities along the boundaries of contiguous habitats (e.g., sympatric populations of *V. bellii*, *V. vicinior*, *V. solitarius*, and *V. huttoni* in the San Bernardino Mountains of southern California; see Grinnell and Swarth, 1913:292). Second, a "stratal separation" of habitat(s) within a plant association (e.g., *V. olivaceus* foraging and nesting in the canopy with *V. griseus* occupying the shrub layer of the same broadleaved, riparian woodlands in the eastern United States; see Hoiberg, 1954:369).

For sympatric species of *Vireo*, this "stratal" type of habitat separation (which may result sometimes in overlap of foraging positions) nearly always occurs between members of different subgenera (i.e., one species having eye-rings and wing-bars while the other lacks such morphological characters). In addition to the example of *V. griseus* and *V. olivaceus* cited above, *V. solitarius* and *V. gilvus* in the western United States seem to have overlapping (regularly?) foraging positions in broadleaved, riparian areas. In southeastern Arizona, Marshall (1957:62) finds that *V. huttoni* (a member of the *solitarius* species group) may occur with these two species in riparian areas. However, *V. huttoni* is normally restricted to oak woodlands with continuous canopy, and, in the western United States, this habitat is usually separate from (but often contiguous to) the habitats of other species of *Vireo* (see Grinnell and Swarth, 1913:292). Of the sympatric species of *Vireo*, the two that appear to coexist within a habitat (habitat co-occupancy) during the breeding season are *V. olivaceus* (arboreal forager) and *V. flavifrons* (arboreal, but strictly crown-layer forager), each belonging to a separate subgenus. My examination of the breeding-bird censuses from eastern and southeastern United States reported in *Audubon Field Notes* during the past seven years indicates numerous occurrences of these two species on the same study tract; unfortunately, no information is available as to the foraging ecology

and breeding positions of these two species in areas where they appear to occupy the same unit of habitat. The "spatial" type of habitat separation appears to be the prevalent condition between sympatric species belonging to the same species group or subgenus (e.g., *V. bellii* and *V. vicinior* in southwestern United States, and *V. gilvus* and *V. philadelphicus* in northeastern United States). Generalizations such as these indicate that a certain divergence in relationship (as suggested by the presence or absence of eye-rings and wing-bars) as well as a difference in foraging positions is manifested (or necessary?) when species of *Vireo* exist in close proximity to one another.

It would seem, then, that within the genus *Vireo* selection has operated for occupation (at least during the breeding season) of separate habitats rather than for habitat co-occupancy in achieving the necessary ecological (and ethological?) compatibility required if previously isolated forms are to develop sympatry upon contact. Since this type of sympatric relationship results in each species having its breeding and feeding positions spatially separate from those of other species, the necessity for different ethological isolating mechanisms would be much reduced. Thus, it is not surprising that the members of this genus are mostly uniform, plain-colored species showing little diversity in external morphology or general ecology. Admittedly, there is a problem here of "cause or effect"; either the species of a given subgenus or species group have not diverged (in morphology and/or vocalizations?) sufficiently for habitat co-occupancy or the stringency of habitat selection (resulting in habitat separation) has eliminated or decreased selection for pronounced ethological isolating mechanisms. Nevertheless, occupation of spatially separated habitats appears to be a generalization applicable to members of both subgenera of *Vireo*, and this study can offer no information on the problem of why selection has favored habitat separation as an "avenue" for the development of sympatry in this avian group. Comparisons with the Palearctic *Parus* have been discussed above. In contrast to sympatric relationships in *Parus* and *Vireo*, it would appear, in the thrush genus *Catharus*, that selection has stressed emphasis on vocal and behavioral modifications—rather than differences in plumage coloration or spatial separation of habitats—as a possible "avenue" for obtaining ethological compatibility in sympatric situations (see Dilger, 1956*b*:347–351).

Little is known about the behavior and general ecology of the various species of *Vireo*. Lawrence (1953) reported some information on the breeding biology of *V. olivaceus*, and Pitelka and Koestner (1942) reported similarly on *V. bellii*. More information on behavior and foraging ecology would be extremely useful, and will be necessary before these generalizations on sympatry and habitat utilization in the genus *Vireo* can be accepted as more than tentative.

Migration Patterns of Vireos

Since all the species of *Vireo* having wide distributions in North and Middle America are migratory (excepting the permanently resident *V. huttoni*), any attempt to correlate intraspecific variation with environmental factors must take into account the climate of the winter quarters as well as that of the breeding quarters. Salomonsen (1955) has discussed the role of migration in relation to intraspecific variation. He points out that within some migratory species the populations breeding in the northern part of the species' range have winter quarters further south than the winter quarters of conspecific populations whose breeding ranges are south of (but contiguous to) those of the northerly breeding populations; the northern populations are thus long-distance migrants and the populations breeding in the lower latitudes are short-distance migrants. A species with such a migration pattern is considered by him to have a "leap-frog" or allohiemic migration pattern. As he further states, the short-distance migrants (having winter quarters north of those of the long-distance migrants) are subjected to colder winter temperatures. From such observations he reasons—in accordance with the heat conservation principle underlying Bergmann's rule—that the populations exposed to colder winter temperatures should be larger, resulting in an apparent reversal of Bergmann's rule. His examination of ringing returns and the distribution of many European species showing reversals of Bergmann's rule have demonstrated that nearly all of these species are "leap-frog" or allohiemic migrants.

Thus, considering "competition . . . for food as the primary reason for wide dispersal in the off-season", Salomonsen (1955:10) has divided migration patterns into two major categories: (1) Synhiemy or the condition whereby the various populations of the same species coexist in a common wintering quarter; (2) Allohiemy or the condition whereby populations within a species have separate (geographically) wintering quarters. Intermediate conditions between these two categories are also recognized by him.

Considering the possible importance of the location of winter quarters on geographical variation, a study of migration within the genus *Vireo* was undertaken. Below is a tentative statement of migration patterns for some of the species of this genus that I have determined on a basis of study of literature, and the "subspecific" allocation of specimens (Mus. Comp. Zool.) taken in winter quarters:

griseus (6 to 9 races)	allohiemic (tandem pattern?)
bellii (4 races)	allohiemic (leap-frog?)
vicinior (monotypic)	synhiemic
solitarius (9 to 10 races)	allohiemic (leap-frog)
flavifrons (monotypic)	?
atricapillus (monotypic)	synhiemic

gilvus (5 to 6 races)	allohiemic (leap-frog)
philadelphicus (monotypic)	synhiemic
olivaceus (10 to 12 races)	allohiemic (leap-frog)

It can be seen from this listing that the allohiemic species are polytypic. Also, each of the allohiemic species demonstrates, in varying degrees, ecogeographical variation. The synhiemic species are monotypic, with their winter quarters unified and rather restricted (excepting *V. flavifrons*) in geographic area. This condition is the expected one, for, as Salomonsen (1955:53) suggests, allohiemic species with geographically isolated populations during the winter will have their various populations exposed to different environments and different selection pressures. Further, it must be remembered that some of these allohiemic species have discontinuous distributions; here, reduction of gene flow between various conspecific populations might facilitate adaptive divergence (viz., climatic adaptation) at the intraspecific level (see Mayr, 1954:160–163). *Vireo solitarius* and *V. gilvus* are allohiemic species consisting of mostly migratory populations; however, both have developed local, endemic populations (*lucasanus* and *victoriae* segments, respectively) resident to the Cape region of Baja California.

The suppressing action of a common winter quarters on intraspecific variation within synhiemic species is possibly illustrated by *V. atricapillus*. This species shows no variation in external morphology although the breeding range is strongly discontinuous, being restricted to isolated foothills in Coahuila, central and western Texas, southern Oklahoma, and southwestern Kansas. Moore (1938:25) has reported the winter quarters of these populations on the coast of Sinaloa. A common wintering area here helps to explain the lack of variation in a monotypic species.

Unlike the other monotypic species, *V. flavifrons* has widespread wintering quarters extending from southern Mexico south to Venezuela and Colombia. The lack of ecogeographical variation in this species does not necessarily imply a common winter quarters for the species, for specimens collected throughout the large, wintering area cannot be compared (phenotypically) with population samples collected throughout the breeding quarters in eastern North America. In a later section of this paper, I suggest that *V. flavifrons* is a "young" species with fluctuating populations and is in process of extending its breeding range. Banding returns may eventually explain the migratory pattern of the populations of *V. flavifrons*.

Geographic Variation in Size

Within the genus *Vireo*, trends of intraspecific variation in size (as indicated by variation in wing length) seem in conflict with Bergmann's rule; little evidence was found for a negative correlation between wing length and temperature. Of the wide-ranging species of this genus, sufficient material

for adequate analysis was available for *V. griseus*, *V. solitarius*, *V. huttoni*, *V. gilvus*, and *V. olivaceus*. Of these species, *V. solitarius*, *V. huttoni*, and *V. gilvus* have the largest wing lengths in the approximate region of northwestern Mexico with smaller wing lengths occurring elsewhere (Tables 2, 3, 4). *Vireo olivaceus* and *V. griseus* (excluding insular populations) demonstrate (Tables 1, 5) north to south clinal decreases in wing length; however,

TABLE 1

MEASUREMENTS[1] FOR *VIREO GRISEUS* SUPERSPECIES

No.	Locality and name of segment	Wing mm.	Bill mm.	Tail mm.	100×bill / wing	100×tail / wing
1.	Southern New England (*noveboracensis*)	64.6 ± 0.6 (11:64–66)	13.6 ± 0.3 (11:13–14)	51.1 ± 1.2 (11:49–53)	21.1	79.1
2.	Virginia to New Jersey (*noveboracensis*)	63.7 ± 0.6 (12:62–64)	13.4 ± 0.4 (12:13–14.5)	50.4 ± 1.4 (12:48–53)	21.0	79.1
3.	Georgia (*noveboracensis?*)	63.5 ± 0.6 (12:62–64)	13.4 ± 0.6 (12:12.5–14.5)	49.8 ± 1.1 (12:48–52)	21.1	78.4
4.	Southern Florida and Keys (*maynardi*)	60.5 ± 1.0 (15:58–62)	15.1 ± 0.4 (15:14.5–16)	48.2 ± 1.1 (15:46–50)	25.0	79.7
5.	Bermuda (*bermudianus*)	58.8 (8:56–60)	15.0 (8:14–16)		25.5	
6.	Kansas (*noveboracensis*)	62.4 ± 0.6 (11:61–63)	13.6 ± 0.4 (11:13–14.5)	50.8 ± 0.9 (10:49–52)	21.8	81.4
7.	Tennessee (*noveboracensis*)	61.2 ± 0.4 (11:61–63)	14.4 ± 0.4 (11:14–15)	48.8 ± 0.9 (11:47–50)	23.5	79.7
8.	Louisiana (*griseus*)	61.3 ± 0.6 (13:60–62)	14.6 ± 0.6 (12:13.5–15)	49.0 ± 1.0 (13:47–50)	23.8	79.9
9.	Brownsville area, Texas (*micrus*)	58.1 (7:57–59)	12.4 (7:12–13)	47.4 (7:46–48)	21.3	81.6
10.	San Luis Potosi (*micrus*)	59.7 ± 0.5 (10:59–61)	13.9 ± 0.7 (10:13–15)	49.1 ± 1.3 (10:47–52)	23.3	82.2
11.	Yucatan and British Honduras (*semiflavus?*)	57.4 ± 1.6 (16:54–59)	14.1 ± 0.9 (16:12.5–15)	47.6 ± 1.3 (16:45–49)	24.6	82.9
12.	Lowlands of Costa Rica (*pallens?*)	55.6 (7:55–56)	14.2 (7:13.5–14.5)	46.4 (7:45–47)	25.5	83.5
13.	Bahama Islands (*crassirostris*)	64.9 ± 2.1 (12:62–70)	15.9 ± 0.6 (12:15–70)		25.3	
14.	Tortuga Island (*tortugae*)	63.7 ± 1.3 (11:61–66)	15.6 ± 0.4 (11:15–16)	50.7 ± 1.3 (10:49–54)	24.5	79.6
15.	Cuba (*gundlachii*)	56.0 ± 1.0 (12:55–58)	15.1 ± 0.5 (12:14–16)	51.3 ± 0.9 (12:50–53)	27.0	91.6
16.	Jamaica (*modestus*)	58.6 (7:57–60)	12.6 (7:11.5–13)		21.5	
17.	Old Providence Island (*approximans*)	61.4 (5:60–63)	15.6 (5:15–17)		25.4	
18.	Cozumel Island (*V. bairdi*)	62.1 (9:60–64)	15.3 (9:15–16)	52.6 (9:50–56)	24.6	84.7
19.	Highlands of Costa Rica (*V. carmioli*)	66.4 (9:64–69)	12.4 (8:12–13)	46.6 (8:45–50)	18.7	70.2
20.	Porto Rico (*V. latimeri*)	65.3 (7:63–67)	13.6 (7:13–14.5)	59.5 (6:58–62)	20.8	91.1

[1] For Tables 1–5, measurements cited as follows: mean to nearest 0.1 mm. plus or minus standard deviation to nearest 0.1 mm. (number of sample: range of sample). Standard deviation not calculated for samples of fewer than ten individuals.

the northern breeding populations of these two species migrate, respectively, to South America and Middle America. The northern breeding populations of *V. solitarius* and *V. gilvus* also migrate to the lower latitudes (Middle America) for the off-season. Populations of *V. huttoni* are resident in evergreen–oak habitats throughout the western United States and Mexico.

Vireo solitarius.—In this species (see Fig. 1 and Table 2), the resident populations (*notius* and *montanus* segments) occurring in British Honduras and Guatemala, respectively, have the smallest wing lengths of all the widely distributed populations of the species. The largest wing lengths are found in breeding populations from the foothills and mountains of northwestern (*pinicolus* segment) and central (*repetens* segment) Mexico; populations of the former segment apparently move south during the winter to central Mexico in the general region of the resident populations of the latter segment. Breeding populations with wing lengths intermediate between the extremes cited above occur in Baja California (*lucasanus* segment) and in temperate North America (*cassinii*, *plumbeus*, *solitarius*, and *alticola* segments). Since most of the migratory populations breeding in North America have winter quarters extending approximately from central and eastern Mexico to the Guatemala–Nicaragua area, they are thus subjected to about the same winter temperatures as the resident populations of that region. According to Bergmann's rule, populations exposed to colder winter temperatures should have larger wing lengths than those having warmer winter quarters; the wing lengths and winter quarters of the populations of segments *solitarius* and *alticola* in eastern North America indicate an allohiemic migration pattern for the two segments which may be interpreted (Salomonsen, 1955:44) as a manifestation of Bergmann's rule. The populations of *V.*

TABLE 2

MEASUREMENTS FOR *VIREO SOLITARIUS*

No.	Locality and name of segment	Wing mm.	Bill mm.	Tail mm.	100×bill/wing	100×tail/wing
1.	New England (*solitarius*)	75.1 ± 0.9 (30:73–77)	13.4 ± 0.4 (27:12–14)	53.6 ± 1.0 (30:52–56)	17.8	71.4
2.	Central Virginia (*alticola*)	79.2 ± 0.7 (24:78–81)	14.4 ± 0.3 (20:13.5–15)	55.9 ± 1.0 (24:54–57)	18.2	70.6
3.	Western North Carolina and South Carolina (*alticola*)	81.2 ± 1.1 (22:80–84)	15.6 ± 0.5 (22:14–16)	55.9 ± 1.0 (22:57–62)	19.2	74.0
4.	Southern British Columbia (*cassinii*)	74.6 ± 1.2 (12:72–76)	14.9 ± 0.7 (12:13.5–16)	54.4 ± 0.9 (12:53–56)	20.0	72.9
5.	Central and southern California (*cassinii*)	76.9 ± 1.5 (14:73–78)	15.1 ± 0.4 (21:14.5–16)	55.3 ± 1.0 (20:53–57)	19.6	71.9
6.	Cape region of Baja California (*lucasanus*)	70.1 ± 1.7 (12:66–72)	15.2 ± 0.4 (29:14–16)	52.1 ± 1.1 (29:50–54)	21.7	74.3
7.	Colorado (*plumbeus*)	77.2 ± 0.6 (11:76–78)	14.8 ± 0.4 (11:14–15.5)	54.9 ± 0.9 (11:53–56)	19.2	71.1
8.	Southeastern Arizona (*plumbeus*)	81.3 ± 1.0 (21:79–83)	15.0 ± 0.6 (21:14.5–16.5)	58.0 ± 1.3 (21:56–60)	18.5	71.3
9.	Sonora (*pinicolus*)	84.7 ± 1.1 (12:83–87)	15.2 ± 0.3 (12:14–16)	62.2 ± 1.0 (12:60–63)	17.9	73.4
10.	Guerrero (*repetens*)	82.4 (7:80–83)	15.9 (7:14–16)	58.7 (7:55–59)	19.3	71.2
11.	Guatemala (*montanus*)	68.5 (4:66, 69, 69, 70)	13, 13	50, 50, 51	19.9	

gilvus have a pattern of geographic variation in wing length (Table 4) similar to that of *V. solitarius*.

Vireo huttoni.—A striking departure from Bergmann's rule is the variation in wing length (Table 3) within *V. huttoni*, the only nonmigratory species of North and Middle American distribution. The largest wing lengths in this species are characteristic of populations (*stephensi* segment) restricted to forested areas of northwestern Mexico; the smallest wing lengths are from populations (*huttoni* segment) resident to southern British Columbia. Intermediate wing lengths are from populations of western United States (*huttoni* segment), northern and northeastern Mexico (*carolinae* segment), central and southern Mexico (*mexicanus* segment), and Guatemala (*vulcani* segment). Here, it is interesting to examine (Table 3) the distributions of all the populations or segments with smaller wing lengths than the *stephensi* segment; these populations with

TABLE 3

MEASUREMENTS FOR *VIREO HUTTONI*[1]

No.	Locality and name of segment	Wing mm.	Bill mm.	Tail mm.	100×bill/wing	100×tail/wing
1.	Southern British Columbia and Washington (*huttoni*) (3500 ft., 36 F.)	62.8 ± 0.9 (14:61–64)	12.2 ± 0.4 (12:12–13.5)	48.2 ± 0.9 (14:47–50)	19.4	76.8
2.	Oregon and northern California (*huttoni*) (4000 ft., 40 F.)	63.5 ± 0.8 (23:62–65)	12.8 ± 0.5 (19:11.5–13.5)	49.5 ± 1.6 (23:47–53)	20.2	78.0
3.	Central California (*huttoni*) (4200 ft., 44 F.)	63.9 ± 0.9 (16:62–65)	12.6 ± 0.4 (15:11.5–13)	50.7 ± 1.1 (16:49–53)	19.7	79.3
4.	Southern California (*huttoni*) (5500 ft., 46 F.)	65.7 ± 0.9 (11:64–68)	12.8 ± 0.5 (11:11.5–13.5)	50.9 ± 1.3 (11:49–53)	19.5	77.5
5.	Cape region of Baja California (*cognatus*) (4000 ft., 55 F.)	66.8 ± 1.1 (15:66–70)	13.4 ± 0.6 (28:12–14.5)	51.5 ± 1.2 (31:48–53)	20.1	77.1
6.	Arizona (*stephensi*) (6200 ft., 45 F.)	66.5 ± 1.1 (16:65–68)	12.9 ± 0.5 (16:12.5–14)	51.7 ± 1.0 (16:50–53)	19.4	77.7
7.	Chisos Mts. in western Texas (*carolinae*)	66.1 (7:63–68)	13.1 (7:12.5–13)	52.1 (7:50–54)	19.8	78.8
8.	Sierra del Carmen, Coahuila (*carolinae*) (7000 ft., 51 F.)	65.6 (9:64–68)[2]	12.9 (9:12–14)	51.4 (9:49–52)	19.7	78.4
9.	Sonora (*stephensi*) (5000 ft., 55 F.)	68.7 ± 1.0 (10:67–70)	13.1 ± 0.3 (10:13–14)	55.5 ± 1.0 (10:54–57)	19.1	80.8
10.	San Luis Potosi (*carolinae*?) (5700 ft., 59 F.)	67.3 ± 1.1 (18:65–69)	12.8 ± 0.4 (18:12–13.5)	52.8 ± 0.8 (18:51–54)	19.0	78.5
11.	Morelos and Federal District (*mexicanus*) (6000 ft., 54 F.)	66.6 ± 1.2 (14:64–68)	13.1 ± 0.6 (12:12.5–14.5)	53.8 ± 0.8 (14:52–55)	19.7	80.8
12.	Southern Mexico (*mexicanus*) (7000 ft., 63 F.)	66.3 (8:65–68)	13.2 (8:13–14)	51.4 (8:49–52)	19.9	77.5
13.	Guatemala (*vulcani*) (5000 ft., 65 F.)	63, 64, 65	12, 12, 12.5	45, 48, 48		

[1] For this species, altitude (accurate to nearest 500 ft.?) and mean temperature (°F.) of coldest month have been estimated and are included here.
[2] Chord measurement.

smaller wing lengths occur in relatively more humid regions to the north, east, and south of northwestern Mexico.

Vireo olivaceus.—Throughout the extensive breeding distribution (roughly, temperate and tropical America) of this polytypic species, there is a north-to-south clinal decrease in wing length of continental populations (New England, 83 mm.; Panama, 79 mm.; Brazil, 67 mm.; see Table 5). The North American populations (*olivaceus* segment) have winter quarters in the Amazon Basin. The Middle American populations (*flavoviridis* and [?] *hypoleucus* segments) have winter quarters extending from Panama to the Amazon Basin. In the region of the Amazon Basin and Matto Grosso, there are resident populations (see Zimmer's discussion, 1941:4–9) which, to my knowledge, have the smallest wing lengths of all the populations of this species. In this species, superficially in agreement with Bergmann's rule, the variation in wing length becomes inconsistent with the rule upon consideration of the location of the winter quarters; many of the populations breeding in Middle America (*flavoviridis* segment) have winter quarters in Panama whereas the North American populations (*olivaceus* segment) with larger wing lengths are "wintering" in the Amazon Basin during the summer of that hemisphere; however, temperature differences at these low latitudes should be of negligible effect. Until more is known about the location of the winter quarters of the populations of this species, all that can be concluded about geographic variation in wing length is that a north-to-south cline for decreased wing length exists when populations from only the breeding quarters are compared. It is possible that the northern breeding populations have an increased wing length as an adaptation for long (and fast?) migration to South America. Variation in wing length (Table 5) within *V. griseus* is similar to *V. olivaceus* in showing (for continental populations) a decrease in wing length from eastern North America south to Panama; in this species, likewise, the pattern of variation becomes difficult to interpret upon consideration of migration and location of winter quarters.

Correlations with climatic gradients.—All attempts to find a negative correlation between temperature and size (Bergmann's rule) within the various species of *Vireo* failed. Several measures of yearly fluctuations in temperature were considered: mean temperature of coldest month, mean temperature of three coldest months, and "lowest recorded temperature." However, the absence of adequate meteorological data for the localities of population samples from Middle America prevented a serious analysis of this possible relationship. Having resident populations distributed over a wide geographic region (southern British Columbia and western United States south through Mexico to the Guatemala area), *Vireo huttoni* is the one species whose various populations are exposed, consistently, to a gradient of decreasing winter temperature from south to north. There appears to be no relationship in this species (see Fig. 2) between wing length and temperature.

Moreau (1957), by use of partial correlation analysis, has presented evidence for a positive correlation between wing length and altitude (independent of effect of temperature) for the African populations of the *Zosterops* complex. My data for intraspecific variation in the species of *Vireo* fail to indicate the presence of such a phenomenon. Of the several species, the resident

V. huttoni could possibly be tested by partial correlation analysis. The scatter diagram (Fig. 3) for wing length and altitude comparisons within *V. huttoni* indicates no relationship between the two variables; however, I lack sufficient data to test the point statistically.

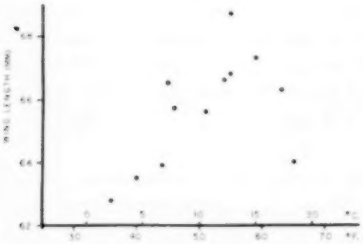

FIG. 2. Variation in wing length in relation to mean temperature of coldest month for 12 populations of the resident *Vireo huttoni* (see Table 3). Note the apparent absence of correlation between wing length (as an index to body size) and cold temperature.

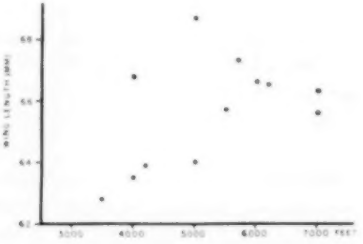

FIG. 3. Variation in wing length in relation to altitude for 12 populations of the resident *Vireo huttoni* (see Table 3). Note the lack of positive correlation between wing length and altitude.

One striking fact which became clear in the course of the study was the location of the populations with the largest wing lengths within the species, *V. solitarius*, *V. huttoni*, and *V. gilvus*. Within each the largest mean wing lengths are from the plateaus and mountains of northwestern Mexico (Sonora), a region relatively more arid than any other within the distribution of each of these species. It became evident that the one feature of the environment of the breeding distributions that was related or correlated (in three species of *Vireo* at least) with the clinal variation in wing length was "humidity" or "aridity." In brief, wing length (presumably an indication of body size) was smaller in humid regions and larger in arid regions (for intraspecific comparisons only). In *V. olivaceus*, it is difficult to explain the observed variation in these terms; however, the populations with the smallest wing lengths are resident in the warm, moist regions of the Amazon Basin. And within *V. griseus* (considering continental populations only) the populations with the smallest wing length (*pallens* segment) are resident in the humid, coastal lowlands of Costa Rica. I have tentatively designated this observation as an "aridity effect" which means, simply, that within wide-ranging species of temperate and tropical distribution there may be a tendency for individuals of populations occurring in hot, arid regions to have greater wing lengths than individuals in hot, humid regions. This observation is not new, for

Ripley (1950:361) and Salomonsen (1955:44–46) have noted or presented evidence suggesting that populations of arid regions may be characterized by larger individuals.

"Aridity effect" or "latitude effect."—I have suggested above that the intraspecific increase in wing length of *Vireo* populations occurring in Sonora, Mexico, may represent a positive response in body size to the "aridity" or low humidity of that region. Readily, a similarity appears between this "aridity effect" and the "latitude effect" as described by Snow (1954*a*) for intraspecific variation in some species of *Parus*. In both genera, the populations with larger wing lengths occur in foothills or mountains of lower latitudes. For both genera, these regions (both approximately 30°N) are in climatically arid areas of northwestern Mexico and northwestern Africa, respectively. However, it must be remembered that both in *Parus* (see Snow, 1952:489–490) and in *Vireo* (see Marshall, 1957:106–107) these populations under consideration occur in the forested elevations of the highlands.

Discussing the relationship between wing length and temperature within the species of *Parus* showing the "latitude effect," Snow (1954*a*:20–21) states "With the same winter temperatures, wing-length tends to be greater at lower latitudes than it is at higher latitudes." Such a relationship with winter temperature is not true for the genus *Vireo*. First, the populations of *V. solitarius* and *V. gilvus* breeding in northwestern Mexico move south during the winter to central and southern Mexico. Second, the *V. huttoni* populations resident in northwestern Mexico (Sonora) are exposed to milder winter temperatures than the populations resident to southern British Columbia.

Snow's interpretation of the latitude effect stresses the importance of feeding ecology with the short day for food gathering during winter in the higher latitudes (Scandinavia) being a critical factor limiting body size. Could this interpretation apply to the species of *Vireo*? It would seem that this is not the case since most populations of *V. solitarius* and *V. gilvus* (and other *Vireo* species) breeding in high latitudes migrate to tropical or subtropical Middle America for the off season. Also, the resident populations of *V. huttoni* extend north only as far as southern British Columbia (50°N)—to about the latitude of southern England or central Europe.

Presence of an Aridity Effect in other New World Species

One value of studying variation and relationships among the species of a genus is the possibility of finding additional parallels or new expressions of evolutionary phenomena which may be characteristic of other genera. This is especially true for comparative studies of intraspecific variation. Considering the well-known parallelism of climatic adaptation at the intraspecific level, the possibility of finding similar "aridity effects" within species of

other avian genera should be considered in that this may represent a modification or suspension of Bergmann's rule.

For this purpose, I have tried to examine (from the literature and with specimens) some wide-ranging North American species with populations occurring (as annual or summer residents) in northwestern Mexico or southwestern United States:

Dryobates pubescens. Downy Woodpecker.—My measurements (mean wing length to nearest 1.0 mm. for males only [number in sample: range of sample]) indicate that the greatest wing lengths in this resident species are from southwestern United States: New Mexico, 104 (7:103–106); Colorado, 104 (8:102–105); British Columbia, 98 (9:97–100); Alberta to Manitoba, 99 (12:97–100); Michigan, 95 (8:93–96); Newfoundland, 95 (9:93–97); New England, 95 (11:93–97); Virginia, 93 (12:92–96); and Florida, 90 (13:88–91). As in some other North American species, the smaller individuals occur in the southeastern United States.

Sitta carolinensis. White-breasted Nuthatch.—Hawbecker's (1948) study of variation in populations of this resident species in the western United States demonstrates a north-to-south cline for increased wing length (Arizona populations, 90 mm.). My measurements for the eastern United States are: Georgia, 88 (10:87–90) and Florida, 86 (12:84–87).

Lanius ludovicianus. Loggerhead Shrike.—Miller's (1931) investigation of this species reveals that the populations with the longest wings (102 mm.) are resident to the arid lowlands of northwestern Mexico (Sonora) and those with the shortest wings (97 mm.) are resident to southeastern United States (mostly lowlands). Populations in other regions (including southern Mexico) have intermediate wing lengths.

Richmondena cardinalis. Cardinal.—The greatest wing lengths in this resident species are also from northwestern Mexico (Sonora lowlands). My measurements: Sonora (Guaymas area), 98 (15:95–100); Texas (Edwards Plateau), 94 (10:92–96); Kansas, 94 (8:92–95); eastern Texas and northern Louisiana, 93 (14:89–94); Florida, 89 (10:87–90); San Luis Potosi, 88 (10:87–90); and Guerrero, 85 (8:83–87).

Salomonsen (1955:44–46) is aware of this tendency for increased wing length in populations of southwestern United States and northern Mexico. Discussing "leap-frog" migration in the Summer Tanager (*Piranga rubra*), he states that the populations (*cooperi* segment) breeding in the southwestern United States are larger than their counterparts (*rubra* segment) breeding in the eastern United States. He also discusses a comparable example for the variation in the Blue Grosbeak (*Guiraca caerulea*), and suggests that the Song Sparrow (*Melospiza melodia goldmani*) and the Red-winged Blackbird (*Agelaius phoeniceus sonoriensis*) are examples of "increased wing lengths in Mexican forms, . . ."

It is my belief that these examples cited as evidence for an "aridity effect" for some North America bird species represent parallel adaptations to the general low humidity and high summer temperatures (as these conditions may affect selective action on general body size) of northwestern Mexico and the southwestern United States. Whether similar "effects" will be found in species of large distributions (extending throughout diverse climatic regions) restricted to other continents remains to be determined. Since adaptation

may represent interactions or conflicts between various selective forces, this "aridity effect" need not hold true for all North American species with comparable distributions. Miller (1931:104) has made the plausible suggestion that increased wing length in *Lanius ludovicianus* is characteristic of populations inhabiting open land or regions of widely spread vegetation. Pitelka (1951:366) concludes the same for the larger, inland races (*superciliosa* and *immanis* segments) in comparing the "*californica*" group of races of the Scrub Jay (*Aphelocoma coerulescens*). It is noteworthy that Pitelka found the smallest wing lengths from the populations of this species resident to Florida. Finally, I find little evidence for the presence of Bergmann's rule, *per se*, within New World species.

Adaptive Significance of Intraspecific Variation in Size

In the previous sections, I have tried to emphasize the relationship between wing length and environmental conditions among the populations within the species of *Vireo* and some other Nearctic species. Examples have been cited from both resident and migratory species. Within migratory species, consideration of geographic location of winter quarters indicates still a relationship between wing length and change in environment. This "aridity effect" represents, as other ecogeographical rules, no more than a correlation between a

Table 4

Measurements for *Vireo gilvus*

No.	Locality and name of segment	Wing mm.	Bill mm.	Tail mm.	100×bill / wing	100×tail / wing
1.	Massachusetts (*gilvus*)	72.4 ± 0.8 (19:71–74)	14.8 ± 0.5 (19:14–16)	51.4 ± 1.1 (19:49–53)	20.4	71.0
2.	North-central United States (*gilvus*)	69.9 ± 0.8 (15:68–71)	14.7 ± 0.6 (13:13.5–16)	50.1 ± 1.1 (15:48–52)	21.0	71.7
3.	Tennessee (*gilvus*)	71.3 ± 0.6 (10:70–72)	14.3 ± 0.3 (10:14–15)	50.1 ± 1.0 (10:48–51)	20.1	70.3
4.	Southern British Columbia (*swainsonii*)	67.6 ± 0.6 (13:66–68)	13.8 ± 0.4 (12:12.5–14)	50.6 ± 0.5 (13:49–51)	20.4	74.9
5.	Oregon (*swainsonii*)	67.8 ± 0.7 (19:67–70)	13.9 ± 0.4 (22:12.5–14)	52.6 ± 0.8 (22:51–54)	20.5	77.6
6.	Central California (*swainsonii*)	68.5 ± 0.9 (10:66–69)	14.3 ± 0.5 (10:13.5–15)	52.5 ± 1.3 (10:51–55)	20.9	76.6
7.	Southern California (*swainsonii*)	69.1 ± 1.1 (16:66–71)	14.1 ± 0.4 (22:13.5–15)	52.2 ± 1.0 (22:50–54)	20.4	75.5
8.	Cape region of Baja California (*victoriae*)	66.7 ± 1.2 (14:65–69)	15.1 ± 0.5 (24:14–16)	51.6 ± 1.2 (24:49–53)	22.5	77.4
9.	Arizona (*swainsonii*)	72.4 (8:70–74)	15.0 (8:14–16)	51.5 (8:49–53)	20.7	71.1
10.	Sonora (*brewsteri*)	73.4 ± 0.9 (11:72–75)	15.1 ± 0.5 (11:14–16.5)	54.4 ± 1.0 (11:52–55)	20.6	74.1
11.	San Luis Potosi (*eleanorae?*)	70.0 ± 1.1 (15:68–72)	14.8 ± 0.4 (15:14–15.5)	49.2 ± 1.0 (15:48–51)	21.1	70.3

character (here, wing length and, presumably, body size) and a changing environment (see Mayr, 1956:105). Since these intraspecific variations are orderly rather than random, selection forces—through unknown mechanisms—must be responsible for the clinal geographic changes.

Scholander (1955) has criticized the "physiological meaning" of the climatic or ecogeographical rules (for homeotherms, in general) by pointing out (p. 22) that variation in insulation is a more efficient method for controlling the loss of heat to the environment than shifts in surface/volume ratios. And his evidence indicates this. However, if change in body insulation (occurring between the peripheral tissues and the environment) were the only selective mechanism involved, we would expect similar body size for individuals from widely separated localities within the species' range, other conditions being equal. The fact remains that there are numerous cases of intra-

TABLE 5

MEASUREMENTS FOR THE *VIREO OLIVACEUS* SUPERSPECIES

No.	Locality and name of segment	Wing mm.	Bill mm.	Tail mm.	100×bill/wing	100×tail/wing
1.	Southern British Columbia (*olivaceus*)	82.0 ± 1.1 (13:80–84)	17.1 ± 0.4 (13:16.5–18)	57.4 ± 0.5 (13:56–58)	20.9	70.0
2.	Montana (*olivaceus*)	81.7 ± 0.9 (10:80–83)	17.1 ± 0.4 (10:16.5–18)	57.6 ± 1.2 (10:55–59)	20.9	70.5
3.	Massachusetts (*olivaceus*)	82.5 ± 0.8 (22:81–84)	16.9 ± 0.5 (22:16–18)	56.6 ± 0.8 (22:55–59)	20.5	68.6
4.	Virginia (*olivaceus*)	81.4 ± 0.9 (16:80–83)	17.1 ± 0.5 (16:16–18)	56.2 ± 0.9 (16:55–58)	21.0	56.2
5.	North Carolina (*olivaceus*)	81.5 ± 0.5 (13:80–83)	17.1 ± 0.3 (13:16.5–17.5)	56.7 ± 1.1 (13:54–58)	20.9	69.8
6.	Tennessee (*olivaceus*)	81.2 ± 0.6 (14:80–83)	18.4 ± 0.5 (14:17–19)	56.1 ± 1.3 (14:53–58)	22.7	69.3
7.	Northeastern Mexico (*flavoviridis*)	81.1 ± 0.6 (12:80–82)	18.8 ± 0.4 (12:18–19.5)	56.3 ± 1.1 (12:55–59)	23.2	69.4
8.	Southern Mexico (*flavoviridis*)	77.9 ± 1.5 (12:75–81)	18.4 ± 0.4 (12:17.5–19)	55.4 ± 1.2 (12:53–57)	23.6	71.1
9.	Guatemala and British Honduras (*flavoviridis*)	79.4 ± 1.3 (14:76–81)	18.1 ± 0.4 (12:17–19)	55.3 ± 0.5 (14:54–56)	22.8	69.6
10.	Panama (*flavoviridis*)	78.6 (7:78–80)	18.4 (7:18–19)	—	23.4	—
11.	Brazil (*solimoensis?*)	67.2 ± 0.9 (10:65–68)	15.7 ± 0.5 (10:15–17)	54.6 ± 1.0 (10:53–56)	23.4	81.3
12.	Florida Keys (*V. altiloquus barbatulus*)	80.5 (8:78–82)	18.5 (8:18–19)	—	24.2	—
13.	Bahama Islands (*V. a. barbatulus*)	80.3 (8:78–82)	19.5 (8:18–20)	—	24.3	—
14.	Grand Cayman Island (*V. a. magister*)	74.6 (5:73–76)	18.0 (5: 18)	—	24.1	—
15.	Hispaniola (*V. a. altiloquus*)	83.0 (8:82–84)	21.4 (8:20.5–22.5)	—	25.8	—
16.	St. Kitts Island (*V. a. barbadensis*)	80.9 (8:78–82)	20.0 (8:19–21)	63.2 (8:62–65)	24.7	78.1

specific gradients for wing length within bird species. How is this to be explained? The next six paragraphs in this section are speculative, and are presented with the hope of stimulating interest concerning the adaptive significance of intraspecific variation:

1. The channels for heat dissipation available to the bird body are convection, conduction, radiation, and evaporation (vaporization). Salt (1952:128) points out that the first two channels are of little or decreased importance (in passerine species, at least), leaving radiation and evaporation as the two primary channels for heat dissipation. Wallgren (1954:65) finds that evaporation represents a larger percentage (at least 40 per cent at 30°C.) of the total heat loss at higher temperatures in two species of *Emberiza*; this is expected since radiation is proportional to the temperature gradient between the body and surrounding environment. Thus, for birds a certain component of the total heat dissipation may be attributed to thermal properties of internal surface tissues (for vaporization) as well as external tissues (for radiation).

2. Concerning the role of evaporation in avian heat loss, it is interesting to examine the work of Bartholomew and Dawson (1953) on respiratory water loss in some birds of arid habitats in the southwestern United States. They find an inverse relationship between mean water loss per unit of body weight and mean body weight in comparing different species of various body sizes; they state (p. 165) "Why smaller birds should lose relatively more water in respiration than larger birds is not known, but it presumably relates to the higher metabolic rates of the former." These observations might be interpreted to indicate that a larger body size is advantageous in hot, arid environments to prevent desiccation via evaporation.

3. In a hot, humid environment, the bird body has the problem of adequate heat dissipation in that the high temperatures necessitate loss of heat by vaporization. Since the inspired air already has a relatively high actual vapor pressure, the body may have difficulty in expiring sufficient respiratory moisture. Selection for a decreased body size here with the relatively increased lung surface might facilitate heat dissipation.

4. In cold or cooler climates, the primary channel for heat loss in birds is presumably radiation. Since basal heat production appears to be the same in tropical as well as arctic forms, change in degree of insulation or change in surface/volume ratios are two possible avenues open to selection. The studies of Scholander and his co-workers (1950) would indicate that the former is more important, at least for comparisons between species. However, the majority of their data for variation in body insulation is from mammals; whether the channels for heat dissipation are the same and of equal importance for mammals *and* birds under similar environmental conditions is not clear. Snow's (1954*a*:20) analysis of variation in wing length in relation to cold temperature among the populations of *Parus major* indicates a clear trend for increased body size with colder winter temperatures that must have some adaptive significance. A study (if feasible!) of geographic variation in body insulation and heat production within a wide-ranging, resident species of bird is badly needed.

5. The phenomenon of altitudinal variation in wing length and body size within bird species should be mentioned. Moreau (1957) has presented statistical evidence for a direct relation between altitude and wing length in African populations of the *Zosterops* complex. He suggests (p. 331) that a larger wing surface (hence larger wing length) in the higher altitudes is associated with reduced air pressure. I would like to suggest that the populations in the lower altitudes are exposed to hotter, more humid climates (in terms of smaller saturation deficits for inspired air) and selection has operated for smaller-sized individuals in the lower altitudes.

6. The scheme for avian intraspecific variation in wing length (as an index to general body size) presented thus far finds—relative to body size in cooler or temperate regions—larger body sizes in the hot, dry regions and smaller body sizes in hot, humid regions. It would be naive to expect this proposed scheme to appear within all species of birds or to appear in comparisons between species restricted to different climates. Discussing such ideas for the variation in the genus *Parus*, Snow (1954*a*:23) states "Obviously at this higher systematic level the different ecological demands are of paramount importance, so that the climatic trends are likely to have been obscured by other adaptations."

The above comments on the adaptive significance of intraspecific variation in wing length and body size in bird species are, of course, conceptual and speculative.

Variation in Wing Shape

That wing shape or configuration may reflect adaptations at the intraspecific level as well as the species level is well known (Rensch, 1934; Kipp, 1936, Meise, 1938). Summarizing his evidence for Palearctic species, Rensch (1934:310) states that within a species the northern, migratory populations may have more pointed and narrower wings than their southern, resident counterparts. And, he continues, this pointed wing may be achieved by a shortening of the tenth (outermost) primary, by a shortening of the primaries behind the wing-tip, or by a lengthening of the primaries of the anterior margin of the wing. Averill (1925:354–355) discusses the relation between the reduced outermost primary and long-distance migration, and points out the prevalence of this phenomenon in the genera *Vireo* and *Hylocichla* and in some other ten-primaried oscines of North America.

Something that should receive more attention in variation studies (see Mayr and Vaurie, 1948:23) is the possibility that migration affects wing length and conflicts or interacts with expressions of climatic adaptation in general body size (as indicated by wing length). One criticism of this study of intraspecific variation in the genus *Vireo* is the absence of a more adequate measure or index for body size (for a fuller discussion of this problem see Amadon, 1943). Because of an absence of specimen weights for most species, mean wing length of the population samples has been used as an indication of body size. While there is no doubt that a larger body is accompanied by a larger wing, it is quite possible that other factors may affect wing length. Adaptation for migration may result in a lengthening or modification of the feathers of the wing-tip thereby altering the relation between body size and wing length. Until adequate series of weights (or bone measurements) are available, such comments as these must be considered as tentative.

The genus *Vireo* is well suited for an analysis of variation in wing shape both within and between species, since it includes completely migratory

species, species with both migratory and resident populations, and completely resident species.

Intraspecific variation.—Comparing (Table 6) migratory and resident populations, the observation that migratory forms have more pointed wings than resident ones appears to be general for the genus. In *V. solitarius*, the populations restricted to Guatemala and Baja California (Cape San Lucas) have less-pointed wing-tips than the northern, migratory populations; this is substantiated by the agreement of several measurements testing the point. Also,

TABLE 6

VARIATION IN SHAPE OF WING-TIP IN SELECTED POPULATIONS OF VIREOS[1]

Species, locality, and migration status		Difference (expressed as per cent of wing length) between longest primary and 2nd	5th	6th	7th	10th
*V. flavifrons**: New England	M	14	7	16	21	34
V. solitarius:						
New England	M	9	4	12	17	34
British Columbia	M	9	3	12	19	30
North Carolina	sM	7	2	10	15	30
Southern California	sM	7	2	10	16	26
Arizona	sM	7	1	9	14	25
Sonora	sM	7	1	8	15	24
Cape of Baja California	R	7	1	7	11	23
Guatemala	R	7	0	5	11	20
*V. philadelphicus**:						
New England	M	8	15	8	17	29
V. gilvus:						
New England	M	9	0	7	14	24
Cape of Baja California	R	9	0	4.5	10	21
Sonora	sM	8	0	4	13	21
*V. olivaceus**:						
British Columbia	M	7	5	13	17	26
Panama	sM	9	3	10	15	23
Brazil	R	11	0	5	8	22
V. hypochryseus:						
Western Mexico	sM(?)	18	0	1.5	4	17
V. griseus:						
New England	M	14	0	3	10	22
Central America	R	15	0	2	4	16
Cuba	R	14	0	0	3	14
V. carmioli: Costa Rica	R	14	0	4	11	20
V. atricapillus: Texas	M	14	0	2	4	16
V. huttoni:						
British Columbia	R	18	0	1.5	6	18
California	R	17	0	2	5	19
Cape of Baja California	R	18	0	1	6	18
Morelos	R	18	0	1	6	19

* Species lacking the outermost primary.

[1] This table represents an attempt to measure geographic variation in the shape ("pointed" to "blunt") of the wing-tip within some of the species of **Vireo.** The difference between the longest primary and the designated primaries (counting from outside to inside) is expressed as per cent of the mean wing length of the sample (five or more male specimens) measured. Thus a "pointed" wing-tip will have increased percentage values. Resident species or populations are indicated by "R"; migratory forms are indicated by "M" with "sM" indicating short-distance migrants for intraspecific comparisons only.

within *V. solitarius*, intermediate values for pointed wing-tip are characteristic of populations (e.g., those breeding in Arizona) having shorter migratory distances than the northern breeding populations. Exceptional to this rule, are the populations of *V. solitarius* breeding in the southern Alleghenies (*alticola* segment) and wintering on the coastal plain of the southeastern United States; these populations have more pointed wing-tips than would be expected for populations approaching resident (see Fig. 1) status.

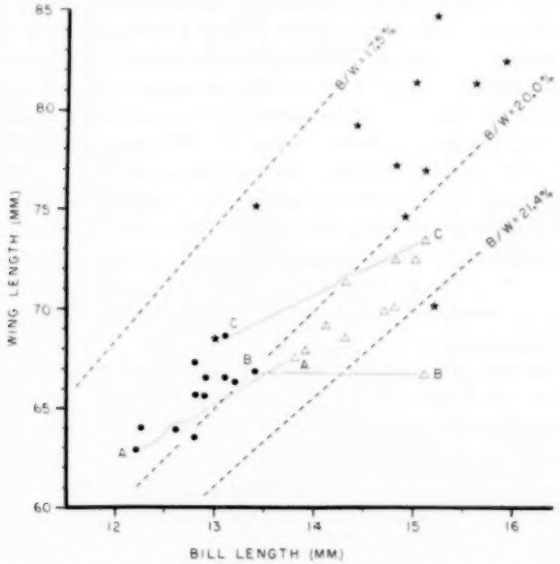

FIG. 4. Relation between wing length and bill length within *Vireo solitarius* (designated by stars), *V. gilvus* (designated by triangles), and *V. huttoni* (designated by black dots). Note the positive correlation between wing and bill length for intra- and interspecific comparisons and the tendency for populations of *V. huttoni* and *V. gilvus* to have relatively longer bill lengths with increased wing length (see Tables 2, 3, and 4). Dashes represent lines of equal bill/wing ratios. Dotted lines connect sympatric populations of *V. huttoni* and *V. gilvus* from the same locality: A, southern British Columbia; B, Cape Region of Baja California; C, Sonora, Mexico.

Vireo griseus, *V. olivaceus*, and, less clearly, *V. gilvus* also show this intraspecific tendency for migratory populations to have more pointed wing-tips. In the species (or superspecies) *V. griseus*, the endemic, allopatric representatives resident to islands of the Caribbean have more blunted or less pointed wing-tips than the populations resident to the mainland of Central America (compare, in Table 6, wing-tip data for Cuban and Panamanian representa-

tives of this complex). This may be due to the longer and stronger isolation of the insular forms from gene-flow as compared to mainland populations. Supporting these observations on the adaptive nature of the wing shape is the lack of variation in wing-tip in resident populations of *V. huttoni*; all these populations have (Table 6) a uniform condition in the wing-tip as shown by the consistency of four measurements.

Comparisons between species.—That migratory species have more pointed wing-tips than resident or less migratory species appears general (Table 6) for the genus and confirms the early work of Averill (1925); I have suggested elsewhere (Hamilton, 1958MS) that the loss of the functional tenth (outermost) primary might have evolved independently in each of three species groups as an adaptation for extensive migration. Comparing the nine-primaried species *V. flavifrons* and *V. philadelphicus* with their ten-primaried, sister species, respectively, *V. solitarius* and *V. gilvus*, it is seen (Table 6) that each nine-primaried species has a more pointed wing-tip than its ten-primaried sister species. Both *V. flavifrons* and *V. philadelphicus* are monotypic, completely migratory species having breeding quarters only in eastern or northeastern North America whereas *V. solitarius* and *V. gilvus* are polytypic, widespread species with breeding quarters throughout North and Middle America.

It is sometimes stated that migratory species have longer wings than resident species (see Dilger, 1956:178) with the underlying implication that a longer wing (through a lengthening of the wing-tip?) is necessary to carry a wing load twice yearly over a migration route than a wing supporting an equivalent load at a resident status. There is little indication that the migratory species of *Vireo* always have longer wings than resident species, although it is difficult to evaluate this because of the divergent effects of strong isolation on wing length in insular representatives of superspecies. *Vireo atricapillus* and *V. philadelphicus* are two completely migratory species which have shorter wing lengths in comparison to the nonmigratory populations of (say) *V. solitarius* and *V. olivaceus*. An adaptation for longer wing in response to migration could mask, as stated above, expressions of climatic adaptation of body size (as indicated by wing length). For the species of *Vireo* there is little evidence for this. Here, it is interesting to compare, for *V. solitarius*, the data of Table 6 with those of Figure 1; it will be seen that the shortest wing lengths are from resident populations of the Guatemalan region *or* the highly migratory populations of northern United States. The largest wing lengths are from populations in northwestern and central Mexico which are, respectively, short-distance migrants and resident populations. The populations of *V. gilvus* show a comparable relationship.

In summary of this section on variation in wing shape, it is evident for

the genus *Vireo* that migratory species or populations have more pointed wing-tips than their resident equivalents. There appears for the genus no noticeable conflict between this rule and climatic adaptation of body size (as indicated by wing length) at the intraspecific level, with the possible exception of *V. olivaceus* (discussed above, p. 320). Since populations which are short-distance migrants have wing-tips intermediate in shape between those of conspecific, migratory and resident populations, it would appear that a pointed wing-tip represents an adaptation for strong migration. "Strong migration" is a vague term in need of clarification; whether a pointed wing is an adaptation for long-distance flight and support of wing load or an adaptation for rapid or more efficient flight remains uncertain. No tendencies for a longer wing associated with migration are present for comparisons between species.

Variation in Tail Length

The meaning and evidence of intraspecific variation in tail length within avian species is not clear. Since the tail feathers are not vascularized or important for heat dissipation, it would be difficult to see a response to cold temperature in the manner of Allen's rule even if there were evidence for decreased tail lengths in the colder regions within species. There is virtually no evidence of this; in fact, Snow (1954*a*:23) has demonstrated for some species of *Parus* a marked tendency for populations in the coldest parts of a species' range to have relatively longer tails.

For intraspecific variation in tail length in the genus *Vireo*, there is (as expected) a positive correlation (see Figs. 5 and 7) between tail and wing length within all species for which sufficient data were available. Considering geographic patterns of variation, there is no evidence for a relatively longer or shorter tail being independently related to climatic conditions within the genus. In that most of these species are residents of or migrants to the lower latitudes, this observation might be expected. However, the resident populations of *V. huttoni* might be expected to show clinal tail length values in response to climatic changes. Indeed, the smallest tail length values of this species are from populations resident in southwestern British Columbia, but here, scatter diagram analysis (Fig. 5) reveals a positive relation with wing length for all the populations of the species. Also, for comparisons between species, the direct relation between tail and wing length is apparent.

In his study of intraspecific variation in *Junco*, Miller (1941:357) found a close and direct relationship between tail and wing length, and Vaurie's analysis (1953:465) of variation in the Muscicapini indicates the same. My examinations (by scatter diagram analysis as in Fig. 5) of tail and wing length data from some studies of intraspecific variation in North American species indicates, as expected, a positive relationship between tail and wing

length; in these various species, aberrant values are from populations showing, clearly, the effect of strong isolation. Lunk's (1952:13) analysis of variation in tail/wing ratio within the Carolina Chickadee (*Parus carolinensis*) and the Black-capped Chickadee (*P. atricapillus*) clearly shows this positive relationship between the two characters and demonstrates a tendency for the populations with longer wings to have larger tail/wing ratios; this suggests that with a larger body size (as indicated by wing length) there may occur a relatively longer tail. Moreau (1955:336) finds the same increase in tail/wing ratio (relative tail length) with increase in wing length in the African *Zosterops* complex. Snow (1954*a*:23) presents data for intraspecific variation in relative tail length for three species of *Parus*, indicating a tendency (both within and between species) for increased relative tail length in the colder regions of the Palearctic. He states that a long tail is an adaptation to cold climate. He cites, however, only values for tail/wing ratios; scatter diagrams of his data for absolute tail length and wing length might show the tendency for relatively longer tails with increase in wing length.

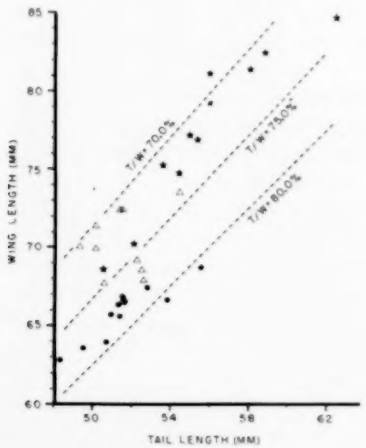

FIG. 5. Relation between wing and tail length within *V. solitarius* (designated by stars), *V. gilvus* (designated by triangles), and *V. huttoni* (designated by black dots). Note the positive relation between wing and tail (see Tables 2, 3, and 4).

This direct relationship between tail and wing length within the species of *Vireo* and other avian species is expected; with a change in body size, there is a corresponding change in tail length necessary for maintenance of body proportions and proper mobility of the organism. Also, in some cases there

appears to be an allometric relation for a relatively longer tail associated with the larger body size (? in the meaning of Huxley, 1932:204–216). However, since adaptation represents a compromise between various selection forces, modifications or suspensions (such as found by Snow?) of an "allometric effect" would be expected. Thus intraspecific variation in relative tail length may be determined—in part—by variation in body size and may not represent (in lower latitudes?) the direct response of an external appendage to the selective forces of the climate.

Variation in Bill Length

An attempt to explain the observed variation in relative bill length (bill/wing ratio) within the species of *Vireo* in direct relation to cold temperature (Allen's rule; see Mayr, 1942:90) was not satisfactory for most species. Because migration to warmer climates for the off season is characteristic of most species or populations breeding in the high latitudes, an absence of climatic adaptation for some characters may be expected. Discussing such problems, Rensch (1952:141) has pointed out that characters changing in correlation with environmental gradients will be more pronounced in species or populations exposed to the severe winters of the higher latitudes rather than to the winters of the tropical regions. The species of *Vireo* (for which data are available) all show (see Figs. 4 and 6) the expected positive relationship between bill and wing length much the same as for tail and wing length (Fig. 5). It is not the purpose of this paper to go into a detailed discussion of variation in bill length; however, some comments on variation in relative and absolute lengths seem appropriate.

Vireo solitarius.—In this species (see Table 2), the shortest bills are found in populations resident to the Guatemalan region and from populations breeding in northern United States and migrating to Middle America for the winter. The longest bills are from populations breeding in northwestern Mexico and wintering in central Mexico. The next longest bills are from populations that winter on the coastal plain of the southeastern United States (see Fig. 1). In that these populations are probably exposed to lower winter temperatures than populations of other segments of the species (such as the resident *montanus* segment in Guatemala), a larger absolute and relative bill length here indicates a marked conflict with Allen's rule. Examining the scatter diagram (Fig. 4) for bill and wing length in this species, a direct (but not strong) relation is observed. The resident populations (*lucasanus* segment) of the Cape region of Baja California have divergent values (absolute and relative) for bill length in comparison to populations of other segments of the species.

Vireo gilvus and *V. huttoni.*—In both these species, variation in bill length (see Fig. 4 and Tables 3 and 4) is positively correlated with wing length with a tendency for the populations within each species to have relatively longer bills (larger bill/wing ratios). In examining Fig. 4, it is of interest that the population (*victoriae* segment) of *V. gilvus* from the Cape region of Baja California represents a clear departure from the pattern

of variation for that species. The dotted lines in Fig. 4 connect populations from each of these two species which are taken from approximately the same locality. In each of these three examples there is a marked difference in bill and wing relation between sympatric populations of the two species. However, the populations of the two species taken from the Cape region of Baja California have approximately the same wing length (and, presumably, same body size); here, the bill lengths of the two populations are noticeably different with the population (*victoriae* segment) of *V. gilvus* showing divergence from the scatter-diagram distribution of points. The Cape of Baja California is the only locality to my knowledge where these two species are sympatric and resident throughout the year. At least for mainland areas, the habitats of *V. huttoni* (evergreen–oak) and *V. gilvus* (riparian broadleaf) are well separated, although often contiguous. Unfortunately, little is known about the habitat distribution of the vireos in this isolated region at the Cape of Baja California, and the suggestion that interspecific competition may have been responsible for the larger bill of the local population of *V. gilvus* is only speculation.

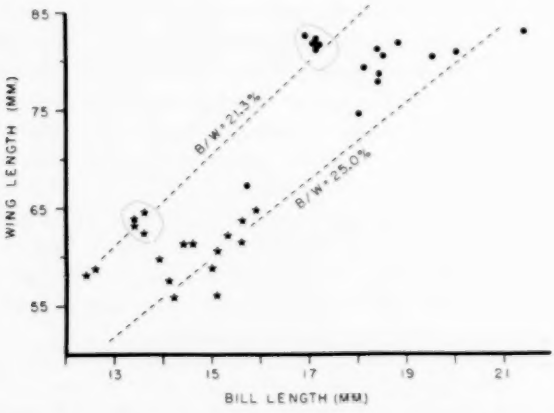

FIG. 6. Relation between wing and bill length within the semispecies *V. griseus* (first seventeen populations of Table 1 designated by stars) and the superspecies *V. olivaceus* (designated by black dots, see Table 5). Note the weak, positive correlation between wing and bill and the tendency for North American populations (enclosed by dotted lines) to have relatively smaller bill lengths.

V. griseus and *V. olivaceus*.—Scatter-diagram analysis for each of these two species or two superspecies (see Fig. 6 and Tables 1 and 5) reveals the expected (but weak) direct relation between bill and wing length except for the populations breeding in North America. The strongly isolated, insular representatives of the Caribbean area show the tendency for insular populations to have greater wing lengths and relatively longer bill lengths (see Murphy, 1938). In both species, the populations breeding in eastern and northern North America have shorter bills than would be expected for their wing lengths. Superficially, this appears as a manifestation of Allen's rule; however, these

northern-breeding populations of *V. griseus* and *V. olivaceus* migrate to Central and South America, respectively, for the off season. I have no satisfactory explanation for this phenomenon. Earlier in this paper (p. 320), I discussed the unexpected (in terms of migration and climate of winter quarters) clinal increase in wing length toward the higher latitudes in *V. olivaceus*. It may be that wing length is "longer" in the higher latitudes rather than bill length is "shorter." The difficulties of interpreting appendage lengths when expressed as percentages of other appendages (such as wing length) is readily seen here (see Amadon, 1943:165).

In summary of this section, bill length is positively correlated with wing length as would be expected. Modifying this relation in *V. griseus* and *V. olivaceus* (as superspecies) is a tendency for the populations breeding in North America to have smaller relative bill lengths; since these populations are migratory, it would be difficult to interpret this condition as an action of Allen's rule. Within several species (*V. huttoni* and *V. gilvus*), there is

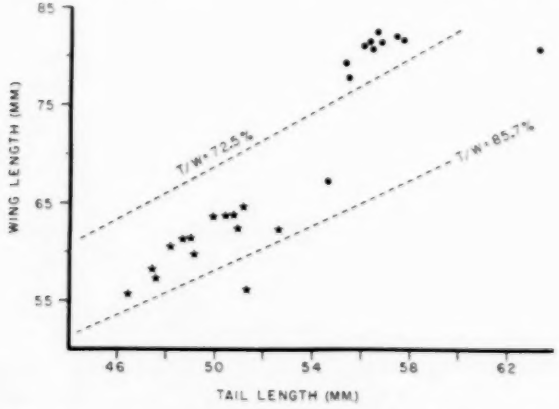

FIG. 7. Relation between wing and tail length within the semispecies *V. griseus* and the semispecies *V. olivaceus* (see Tables 1 and 5). Note the weak, positive correlation between wing and tail.

an indication of an allometric relationship with the populations of larger wing lengths having larger relative bill lengths; the same appears to be true for comparisons between some species. For the genus *Vireo*, Allen's rule does not seem to be important as a factor in climatic adaptation.

GEOGRAPHIC VARIATION IN COLOR

The characteristic pigments of vireos are melanin (gray) and lipochrome (yellow) which occur primarily in the dorsal and lateral (side and flank) feathers. An absence of pigments from the feathers of the throat and breast

and/or belly and under tail coverts occurs in many species. Varying degrees of deposition of melanin and lipochrome are responsible for the coloration of the back feathers, which may vary from yellow to yellow-greenish to gray in different species. Melanin is the predominant pigment in the wing, tail, and head feathers. Species characters, such as eye-stripes, eye-rings, and wing-bars, usually are white, representing an absence of pigment, although in several species (*V. griseus* and *V. flavifrons*) the feathers of the eye-rings are yellow, showing clearly an absence of melanin in comparison to other feathers of the head.

Black coloration occurs in the crown and auricular feathers of *V. atricapillus*, a species restricted to warm, arid regions. The two species showing the most intense yellow coloration (as a character not varying geographically) are *V. carmioli* and *V. hypochryseus*. *Vireo carmioli* is a thicket-forager restricted to the cool, moist highlands (8,000 to 10,000 ft.) in Costa Rica and western Panama. *Vireo hypochryseus* is endemic to western and southwestern Mexico and occurs in broadleaved woodlands of the tropical deciduous vegetation zone. Brown and red pigments are rare among the species of the genus, with rufous or cinnamon coloration appearing in the feathers of *V. bairdi* on Cozumel Island.

Intraspecific variation in color. For the wide-ranging species of the genus, intensity of color or pigment deposition increases with environmental humidity in concordance with Gloger's rule. The adaptive significance of such a phenomenon is unknown. In that most *Vireo* species of North American distribution are migratory, a study of color variation in relation to humidity is hampered by a lack of knowledge of the climate of the wintering quarters of migratory populations.

In *V. solitarius*, melanin deposition in the back, rump, and wing feathers is most intense in populations of *cassinii*, *solitarius*, *alticola*, and *montanus*, which are restricted (except southern breeding populations of *cassinii* segment) to relatively humid regions throughout the year, in comparison to the "paler" segments occurring in the interior of the continent. Of the four "dark" segments, the populations of *solitarius* and *alticola* have "bluish" crown feathers which are noticeably darker than those of *cassinii* and *montanus*.

Populations of *V. solitarius* from the Cape region of Baja California (*lucasanus* segment), southwestern United States (*plumbeus* segment), and northwestern Mexico (*pinicolus* segment) have pale colorations (light melanin depositions) and are listed here in order of decreasing darkness of the back feathers. Populations of the *pinicolus* segment are the lightest in color and are restricted to northwestern and central Mexico throughout the year, an area that is the most arid of the regions in which populations of *V. solitarius* occur. Populations of the *plumbeus* segment, although wintering south

to central Mexico, breed from Wyoming through the Rocky Mountains to western Mexico; thus they are not subjected to the summer aridity of northwestern Mexico (as those of the *pinicolus* segment) or to the humidity of the Pacific coastal region (as populations of *cassinii*). Populations endemic to the Cape region of Baja California (*lucasanus* segment) are resident throughout the year, and, although restricted to a climatically arid region, occur in an area of high relative humidity (in comparison to the Mexican mainland at that latitude) due to the maritime position of the Cape (Dr. C. F. Brooks, pers. comm.). Correspondingly, these populations are slightly darker than the other two "pale" segments. Populations of *V. s. repetens* of central Mexico have not been discussed because of a lack of comparative material.

This geographic pattern of variation in melanin is generally the same for other polytypic species of *Vireo* having wide, continental distributions. *Vireo gilvus*, with a geographic distribution similar to that of *V. solitarius*, has essentially the same expression of Gloger's rule except for the populations restricted to the Cape region of Baja California (*V. g. victoriae*) which are unexpectedly lighter in coloration. *Vireo olivaceus*, *V. bellii*, and *V. griseus* show little expression of Gloger's rule for melanin variation. I am not familiar with the coloration of the *pallens* segment of the *V. griseus* complex.

Yellow pigment was found in *V. solitarius*, *V. huttoni*, and *V. gilvus* to be increased in the back and lateral feathers in populations breeding in humid regions, and decreased in intensity of deposition in the populations or segments restricted to arid regions of the interior. For continental populations of *V. olivaceus*, *V. bellii*, and *V. griseus* the same was true, although less markedly for the latter two species. In *V. solitarius*, the populations breeding in eastern North America (*solitarius* and *alticola* segments) have brighter yellow flank feathers in comparison to populations of other segments (that is, *montanus* of the Guatemalan region) occurring in humid areas.

In summary, melanin and lipochrome are the predominant pigments within the genus *Vireo*. The polytypic species with wide, continental distribution show variation in color (intensity of both pigments) in agreement with Gloger's rule. At the species level, no correlation between color and the inhabitation of a particular climate is apparent. Yellow pigment appears to be a labile character in the genus, occurring within species as an expression of Gloger's rule and occurring in different species as a species character not varying geographically. The presence or absence of pigments appears to be one method that selection has utilized for species recognition characters in the external morphology. The only evidence for coloration of species or populations blending with the habitat or environmental background is the general "greenish" hue in many species which is fairly similar to that of the foliage of the species' habitats.

Interspecific Relationships

Since the results of a study of species relationships in the genus *Vireo* are being prepared for publication separately, an account of the habitat preferences and possible interspecific relations of all the species will not be presented here. However, in the course of the study it was possible to postulate in several cases the species which probably gave rise to other species also now existing. *Vireo griseus* on the mainland of eastern North and Middle America appears to be the only mainland species (other than *V. olivaceus*) which has successfully colonized the islands of the Caribbean. Some of these island representatives are still fairly similar to mainland forms both in morphology and ecology; however, on some of the islands there are "divergent" representatives (e.g., *V. osburni* and *V. nanus*). These examples demonstrate clearly that populations become isolated from the parental body of populations and undergo speciation and divergence. This speciation process may or may not result in modifications of the morphology and/or general ecology. For the species of *Vireo*, the modifications (here "modification" is used in comparison to the parental species) of morphology are of two general types: first, changes in species characters, such as emphasis or loss of coloration (change in intensity), eye-rings, and wing-bars or, second and more rarely within the genus, a change in bill structure associated with change in feeding ecology.

Among the members of the genus on the mainland of North and Middle America, there is an example of the possible origin and divergence of one species from another resulting in two species which are now sympatric; since so little information is available on the factors promoting the divergence of continental species, I am offering—in the following paragraphs—a postulated origin of *V. flavifrons* from *V. solitarius* in terms of their morphological characters, ecological relations, and geographic distributions both in breeding and wintering quarters. Part of this discussion is concerned with the hypothetical results of interspecific competition; for accounts of the meanings and evidence for competition the reader is referred to Gause (1934) and the various papers of Lack (particularly 1944).

Vireo solitarius.—This species is a ten-primaried, polytypic species having a broad breeding distribution throughout forested North and Middle America; it has a wide habitat tolerance (in comparisons with other members of this genus) with the various populations utilizing broadleaved or mixed broadleaved–conifer habitats for foraging in both crown and understory layers. All populations of the various geographic segments of this species have white eye-rings, white wing-bars, and white ventral feathers. The species demonstrates geographic variation in color in accordance with Gloger's rule with populations (*pinicolus* segment) breeding in northwestern Mexico showing almost a complete absence of yellow pigment. Populations from northeastern (*solitarius* segment) and southeastern (*alticola* segment) United States have yellow flank feathers and show,

in the dorsal feathers, a marked decrease anteriorly in yellow pigment resulting in an appearance of a yellow-greenish rump blending into a grayish color for the back. The other component of the back coloration, melanin, increases anteriorly giving a "bluish" color to the crown, nape, and auricular feathers. Populations of this species from other segments (e.g., *montanus* in Guatemala) restricted to humid regions fail to show such intense yellow flank and rump feathers or dark crown feathers.

Vireo flavifrons.—This species is sympatric with the "blue-headed" populations (*solitarius* and *alticola* segments) of *V. solitarius*; in their region of geographic overlap (either in breeding or wintering quarters) these sympatric species are always separated by habitat. The breeding quarters of *V. flavifrons* are restricted to the eastern United States and southeastern Canada; in the breeding quarters, this species is strictly a crown-layer forager of deciduous, broadleaved forests. This species has a more pointed wing (Table 6) than *V. solitarius*, lacks a functional tenth (outermost) primary, and has more distant winter quarters (south to Colombia and Venezuela) than any population of *V. solitarius*. *Vireo flavifrons* is monotypic, the various populations showing no appreciable variation in color. Yellow pigment is restricted to the anterior half of the body with bright yellow throat and breast feathers and yellow eye-rings being characteristic of the species. In the dorsal feathers, yellow pigment increases anteriorly, presenting the appearance of a yellow-greenish head and a grayish rump; the stomach, abdomen, flank, and tail feathers have no yellow pigment.

Origin of Vireo flavifrons.—Apart from the differences stressed above, the two species (considering sympatric populations) are fairly similar in size and in expression of morphological characters, such as eye-rings, wing-bars, and bill shape; also, they are similar in that both are arboreal foragers, and Saunders (1951:165) has called attention to their similarities in song. In the systematic listings of the species of the genus, the two are always placed next to one another, and Bent (1950:285–286) has commented on their close relationship. Because of certain similarities and differences in the external morphology and in the ecology (cited below), I suggest that *V. flavifrons* is derived from *V. solitarius*, and that upon coming into contact after spatial isolation there was selection on the populations of *V. flavifrons* for restriction of foraging position to mostly crown layers of broadleaved forests (ecological isolation).

During the period of spatial isolation, the *V. flavifrons* isolate would have developed a certain genetic reorganization which was sufficient to provide effective reproductive isolation. An important point of this discussion is how much ecological and behavioral (expressed as morphological and/or vocal modifications) divergence occurred in *V. flavifrons* while in isolation; from the examples of isolated representatives of the *V. griseus* complex in the Caribbean, it is apparent that some divergence (at least in plumage coloration and/or feeding ecology) may (or may not) occur while in isolation. The yellow throat and chest of *V. flavifrons* is a unique pigment pattern for the genus, and it might well function as an ethological isolating mechanism. Several aspects of this possibility should be discussed. First, since the two species are now separated by habitat, the differences in morphology (patterns of yellow pigment) between them cannot be serving now as ethological isolating mechanisms for the prevention of hybridization or competition. This, however, does not negate the possibility that at some time in the history of *V. flavifrons* such morphological characters have effectively served as isolating mechanisms.

Second, if such a character as a yellow throat in *V. flavifrons* has acted as an isolating mechanism at some time in the past, did the acquisition of such a character occur during isolation or during early interspecific contacts with *V. solitarius* as a device (see Dobzhansky, 1940:316) for prevention of hybridization? Moore (1957:325–338) has criticized

the case for development of reproductive isolating mechanisms (as characteristics of the entire species) as devices for the prevention of hybridization; he points out that selection may act for differences in the zone of overlap (but for prevention of competition rather than hybridization) and that this does not account for the occurrence of the same isolating mechanisms in populations of either species away from the zone of overlap and contact; finally, he is of the opinion (p. 337) that genetic divergence during isolation "will involve differences that will also serve as isolating mechanisms." The examples of "character displacement" cited by Brown and Wilson (1956:63) for animal species having greater differences in zones of overlap would represent, as they conclude, adaptive differences brought about by interspecific competition acting only on overlapping, sympatric populations.

As stated above, *V. flavifrons* and *V. solitarius* are now almost completely separated ecologically, and it is extremely difficult to attribute both the present ecological differences and the morphological differences (yellow throat in *V. flavifrons* and yellow flank feathers in *alticola* and *solitarius* segments of *V. solitarius*) as results of interspecific competition. However, following Moore's thesis, I have assumed that upon coming into contact with *V. solitarius*, the populations of *V. flavifrons* probably had differences in external morphology (anterior shift in yellow pigment pattern resulting in yellow throat, eye-rings, and crown feathers) which were acquired while in isolation (divergence being facilitated by the small size of range of the isolate?; see below); this anterior increase in yellow pigment then would have provided characters capable of serving as effective ethological isolating mechanisms. (If, as suggested below, these two species were not ecologically separated at the time they established contact, then there also might have occurred selection pressures favoring intensification of the plumage modifications of *V. flavifrons* which, at that time, would begin to serve as isolating mechanisms; see Sibley, 1957:187.) While similar reasoning might be stated for the development of ecological differences between these two species, I shall argue in the following paragraphs that these ecological differences should be attributed to interspecific competition (more accurately: to selection pressures for reduction of competition—see Brown and Wilson, 1956:60).

It appears that for these two species of *Vireo*, selection has ultimately resulted in a separation of habitats rather than co-occupancy of the same habitat in achieving a sympatric relationship. If interspecific competition is considered a factor in this ecological divergence, there is no need to postulate that there was a complete shift from initial habitat co-occupancy to lateral separation of habitats ("spatial habitat separation"). Since populations of both species occur in broadleaved forests in the breeding quarters, at the time of initial interspecific contact there might have been selection on populations of *V. flavifrons* for restriction of foraging positions to crown layers of the habitat (from initial contact to "stratal habitat separation"). Such a vertical, "stratal" segregation of habitats might not have been sufficient in keeping individuals of the two species ecologically separated; selection for utilization of adjacent broadleaved habitats (from "stratal" to "spatial habitat separation") would have completed the ecological (and ethological?) separation of these two species. Supporting—possibly—this argument is the observation for the entire genus, that whenever sympatric species show a "stratal" segregation of habitats, the two species are each from different subgenera (and differ by the presence or absence of eye-rings and wing-bars). As discussed above (p. 313), this indicates that differences in relationships as well as habitat and/or niche requirements are necessary before two species of *Vireo* can have overlap of their respective breeding and foraging positions.

Today there is no evidence that populations of *V. flavifrons* and *V. solitarius* ever come into contact with overlapping, breeding territories in their breeding quarters in eastern United States, and, yet, the two sympatric species may occur as local (but separated) breeders inhabiting, respectively, broadleaved woodlands and mixed broad-leaved–conifer woodlands (see Todd, 1940:476–478). There is some evidence that the populations of *V. flavifrons* undergo fluctuations occasionally (E. Mayr, pers. comm.). Bent (1950:286–287) discusses the shifts in "urban" populations of this species in New England, and Thornton (1951:424) has found this species breeding on the Stockton Plateau of western Texas. *Vireo flavifrons* may be an "infant" species in the process of extending its breeding distribution.

Two other observations tend to support this postulated origin of *V. flavifrons*. First, a hybrid specimen (*V. propinquus*) with characteristics of both *V. flavifrons* and *V. solitarius* is known. I have recently examined the specimen at the U.S. National Museum and agree with Ridgway (1904:167) that the specimen is intermediate in wing structure and coloration between the two species; the noticeable intermediate characters are a very small outermost (tenth) primary, and the yellow breast feathers. The presence of a hybrid individual verifies the close relationship and relatively recent separation of the two species.

Second, Lack has consistently emphasized that as a result of interspecific competition previously isolated species will develop (or increase?) differences in ecology upon coming into contact. Among the agencies furthering ecological divergence, the geographic separation of wintering quarters would appear effective as he (1944:273, 276) has shown for sympatric species occurring (and breeding) in different habitats in England. The same appears true for sympatric populations of *V. flavifrons* and *V. solitarius*. The wintering quarters of *V. flavifrons* extend from Venezuela and Colombia north to Guatemala and southern Mexico. Populations of *V. s. alticola* winter in the lowlands of southeastern United States, and populations of *V. s. solitarius* winter from the coastal plains of southern United States south through eastern Mexico to the Guatemala–Nicaragua area. In the area of overlap of winter quarters, *V. flavifrons* occurs in the lowlands and *V. s. solitarius* is restricted to the highlands. In Guatemala, *V. flavifrons* is found in the lowlands and *V. s. solitarius* occurs in the mountains above 2,000 ft. (Griscom, 1932:317–318). In El Salvador (Dickey and van Rossem, 1938:470), *V. flavifrons* again occurs in the lowlands and *V. s. solitarius* is most abundant at 3,500 ft., but occurs as high as 8,500 ft. Away from the area of overlap of winter quarters, populations of *V. s. solitarius* winter in the lowlands of eastern Mexico. Further south in Costa Rica (where *V. s. solitarius* does not occur), populations of *V. flavifrons* winter in the mountains as well as in the lowlands (Carriker, 1910:781). I have no information on the winter habitats of *V. flavifrons* in northern South America. It would appear then that *V. flavifrons* (in its divergence from the parental *V. solitarius*) has extended its wintering quarters to be geographically separated from the parental species and that populations of the two species have an altitudinal separation of habitats in the region of overlap of winter quarters; whether interspecific competition is (or has been) a factor limiting or affecting the habitat distributions of these two species in the area of overlap of wintering quarters (as well as the geographical separation of off-season distributions) can only by suggested and remains problematic.

Finally, one problem remains to be discussed concerning the postulated origin of *V. flavifrons* from *V. solitarius*. If competition has been operative in increasing the divergence of the two species, why did most of the adaptive change necessary for ecological compatibility between the two species occur in *V. flavifrons* and not *V. solitarius*?

It is probable that the separation (during the Pleistocene?; see Rand, 1948) of the isolate *V. flavifrons* occurred somewhere in the eastern United States. Of importance here might be the magnitude or size of the geographic breeding ranges of the parental species and the isolate; at the time of separation, *V. solitarius* would still have had a wide distribution of breeding populations throughout the remaining United States and Middle America. In a discussion of the evolutionary significance of gene-flow and the peripherally isolated population, Mayr (1954:160–163) suggested that gene-flow from the interior of a species' range acts to disrupt the tendency of peripheral populations to become adapted to local environments and that peripheral isolation may permit an isolate to acquire a new gene-complex adapted to its environment without being "annually disrupted by the infiltration of alien genes and gene-combinations." His theory might be the solution to the problem presented at the beginning of this paragraph. Competition, as postulated for *V. flavifrons* and *V. solitarius*, would result in the action of natural selection on competing populations of both species. However, the competing populations of *V. solitarius* would still be recipient of gene-flow from conspecific populations (away from the area of sympatry with the isolate *V. flavifrons*) thereby diluting selective changes in the genotype for adaptive divergence. This would not be the case for the relatively smaller isolate *V. flavifrons*; these populations (all or a large component of the isolate gene pool) would be more likely to develop genotypes for modification of habitat preferences (and morphological change?) in adaptive response to the selective action of interspecific competition.

This postulated example of morphological and ecological divergence of two related species may be summarized as follows: (1) Initial isolation and development of new gene-complex in the isolate *V. flavifrons*. (2) In *V. flavifrons* while in isolation, morphological divergence which effectively serves as isolating mechanisms upon coming into contact with parental *V. solitarius*. (3) As a result of interspecific competition, restriction of habitat tolerance in *V. flavifrons*. (4) As a further ecological difference, extension of winter quarters in *V. flavifrons* for geographic (and altitudinal) separation from *V. solitarius*. (5) Correlated with No. 4, selection in *V. flavifrons* for wing modification (in response to long migration) resulting in a more pointed wing and loss of the functional tenth primary.

Summary

1. The subdivisions of the genus *Vireo* are briefly discussed; apparently, selection has favored occupation of separate habitats rather than habitat co-occupancy for sympatric relationships.

2. The migration patterns of the various species are delimited according to Salomonsen's 1955 classification.

3. Trends of intraspecific variation in wing length for the genus appear to be in conflict with Bergmann's rule. *Vireo solitarius*, *V. huttoni*, and *V. gilvus* have the largest mean wing lengths in populations breeding in northwestern Mexico. *V. griseus* and *V. olivaceus* have smaller wing lengths (comparing continental populations) in the humid, tropical regions. Evidence for

similar "aridity effects" (greater wing lengths in hot, arid regions and smaller wing lengths in hot, humid regions) for variation within other New World bird species is presented.

4. Speculations are made concerning the adaptive significance of such an "aridity effect."

5. For both intra- and interspecific comparisons, migratory forms have more pointed wing-tips than resident forms.

6. Intraspecific variation in tail length is positively correlated with wing length.

7. The variation in relative bill length does not accord with Allen's rule for climatic adaptation within the genus.

8. Within the wide-ranging species of *Vireo*, variation in intensity of melanin and lipochrome supports Gloger's rule.

9. The relationship between *V. flavifrons* and *V. solitarius* is analyzed; it is suggested that some of the ecological differences between the two sympatric species may be attributed to interspecific competition.

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TERRITORIAL BEHAVIOR OF WINTERING RED-HEADED WOODPECKERS

BY LAWRENCE KILHAM

TERRITORIES of Red-headed Woodpeckers (*Melanerpes erythrocephalus*) were studied near Seneca, Montgomery County, Maryland, where a winter population was attracted to pin oaks (*Quercus palustris*) growing near the Chesapeake and Ohio Canal and the Potomac River. These woodpeckers appeared in September, 1956, and left in May, 1957. Their breeding grounds were unknown. The winter territories were small, well-defined, and represented areas in which individual woodpeckers stored considerable numbers of acorns which they guarded in an aggressive fashion. This defense was well advertised. The striking colors of the Red-headed Woodpeckers, their "quirr, quirr," notes which suggest those of a watchman's rattle, and their pugnacity made them readily seen and heard. A previous communication (Kilham, 1958*b*) describes how these woodpeckers gather pin oak acorns, then conceal their stores from acorn-eaters, such as Blue Jays (*Cyanocitta cristata*) and Tufted Titmice (*Parus bicolor*), by sealing them in with pieces of bark and of wet, rotten wood. Two factors that enabled me to map out the storage territories in some detail were conflicts resulting from the aggressive behavior of the woodpeckers, and a particular patch of woods that offered unusual opportunities for observation. I made some initial studies in winter seasons from 1951 through 1953. More intensive observations involving all species of woodpeckers in the area, extending through 12 months of the year and including visits at dawn and at dusk, were made in 1956 and 1957.

THE STUDY AREA

Creek Wood (Fig. 1) was a patch of woods approximately 215 yards long and 95 yards wide which extended on either side of a small creek from a dirt road on its southern border. Fields surrounded the wood in other directions. This woodland of approximately 4 acres contained the winter territories of 12 Red-headed Woodpeckers. Several features of terrain favored observations (Fig. 2). First, the fields sloped toward the creek so that one could look into the woods at mid-tree elevation and, second, pasturage of cattle in summer gave the woodland an open, park-like character, free of undergrowth and low limbs. Observations of territorial boundaries were further aided by the flashing of the black and white pattern of the Red-headed Woodpeckers against a background of grey, leafless trees. The trees were of medium height and consisted of pin oaks, ash (*Fraxinus americanus*), and black locusts (*Robinia pseudo-acacia*). Red-headed Woodpeckers used dead elms and locusts for excavation of roost holes and for storage of acorns. I made addi-

tional observations on these woodpeckers in bottomlands along the canal. In this area, however, high, tangled woods and a flat terrain made delineation of winter territories almost impossible.

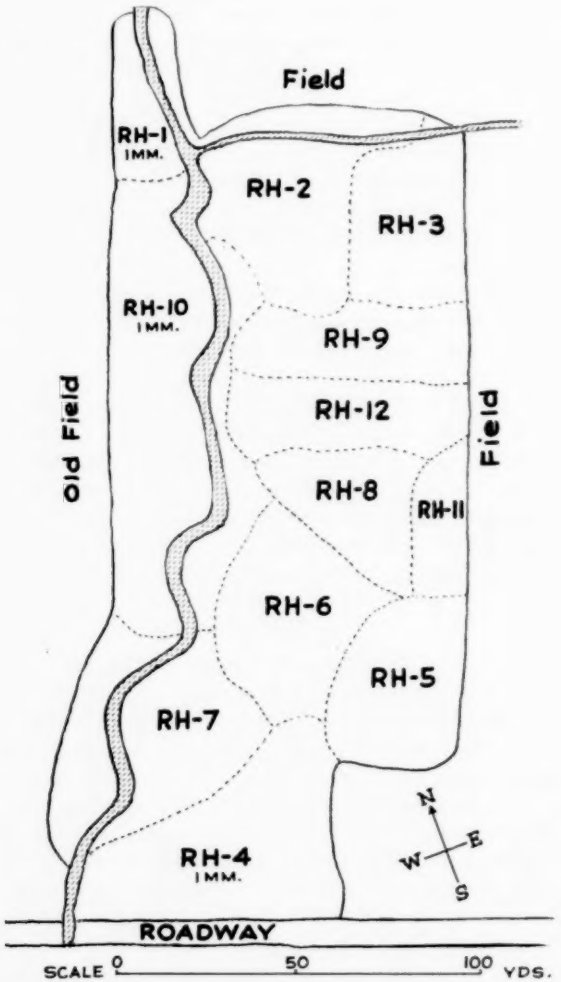

FIG. 1. Diagrammatic map of Creek Wood showing individual territories of 12 Red-headed Woodpeckers (RH = Red-headed Woodpecker; IMM. = immature bird.)

Aggressive Behavior

Red-headed Woodpeckers are agile fliers and they were swift when attacking intruders on their territories. In between attacks they did much "bowing" and calling of "quirr" notes. The woodpeckers spread out their wings and tails and their calls became high-pitched when they were especially excited. This latter display was evoked only by intruders of their own species. Birds intruding on the woodpeckers fell into related and unrelated groups of competitors:

Attacks on other species of woodpeckers.—I saw Red-headed Woodpeckers attack and drive away all the other local species of woodpecker at one time or another. The Pileated (*Dryocopus pileatus*) and Hairy (*Dendrocopus villosus*) woodpeckers, and the Flicker (*Colaptes auratus*), however, were seldom present in Creek Wood. Yellow-bellied Sapsuckers (*Sphyrapicus varius*) were exceptional in being tolerated. They hardly could be classified as competitors since they didn't eat acorns and they drilled holes from which Red-headed Woodpeckers took sap when it flowed. One Red-headed Woodpecker (RH-7, Fig. 1) sometimes rested within a few feet of a sapsucker which made regular visits to a pin oak within its territory. Red-headed Woodpeckers concentrated their attacks on the two remaining species, the Downy (*Dendrocopus pubescens*) and Red-bellied (*Centurus carolinus*) woodpeckers. I never observed that Downy Woodpeckers ate acorns but they doubtless incited Red-headed Woodpeckers by moving up and down over trunks and limbs where acorns were stored. The Red-bellied Woodpeckers, on the other hand, were real competitors. They not only gathered and stored acorns from pin oaks but also occupied the same habitats as the Red-headed Woodpeckers until the latter drove them out in the fall. The Red-headed Woodpeckers seemed to go out of their way to drive off a Red-bellied Woodpecker, more so than for any other bird. On January 5, 1957, for example, I was in a field by Creek Wood when a Red-bellied Woodpecker, carrying an acorn in its bill, flew out from the territory of a Red-headed Woodpecker (RH-10). RH-10 immediately pursued the intruder well out over the field. On January 26 I watched a Red-headed Woodpecker at the Dierson Wildfowl Refuge fly over 100 yards, on two occasions, to drive a Red-bellied Woodpecker from a fringe of trees along the Potomac.

Attacks on non-piciform birds.—Red-headed Woodpeckers attacked Blue Jays and Tufted Titmice which, as elsewhere described (Kilham, 1958*b*), were their principal competitors for stored acorns. Another type of competition was for holes in trees. Each Red-headed Woodpecker had one main roost hole within its territory and, not infrequently, a number of alternates. Competition for these holes began when Starlings (*Sturnus vulgaris*) appeared

in mid-January, the male Starlings flapping their wings and giving their screechy songs. Red-headed Woodpeckers were having little rest by the end of the month. They swooped back and forth with excited "quirrs." Three or four Starlings would perch near a roost hole at one time or in relays. They were tough and persistent. A Red-headed Woodpecker might attack them again and again, occasionally hitting one with the full impact of a swoop, but the Starling involved would only shift its perch by a few inches.

Two encounters may serve to demonstrate the intensity of this competition. On January 26, 1957, a Red-headed Woodpecker struck a Starling directly and the two birds fell 40 feet to the ground as they grappled together. I heard a yelp from one of them. The woodpecker flew up straight away, but I was unable to determine what happened to the Starling. On March 17, I was searching for RH-1 at 5:00 p.m. There was no sign of this Red-headed Woodpecker in its territory. Then I heard noises and scratches coming from RH-1's roost hole which was 12 feet up, at the base of a broken branch. When I threw a log at the tree RH-1 flew out followed by the Starling. A fight had gone on within the roost hole. As spring advanced, I never encountered an instance in which Starlings succeeded in dispossessing a Red-headed Woodpecker. Red-bellied Woodpeckers did not do so well. They were paired and were excavating nest holes in early spring (Kilham, 1958*c*) at a time when Red-headed Woodpeckers carried on as single birds. The Red-bellied Woodpeckers fought, but all eight pairs under observation lost out in the face of Starling competition.

Determination of Territorial Boundaries

Creek Wood was occupied by 12 Red-headed Woodpeckers. On repeated week-end visits I observed that these woodpeckers rarely made excursions outside of the woodland, and that they remained close within individual areas. It thus became apparent that the borders of Creek Wood were natural boundaries for many of the Red-headed Woodpeckers. Accordingly I concentrated on the problem of determination of territorial boundaries lying within the woodland. Observations made for this purpose over a number of months fell into the following six categories:

(A) Recognition of individual Red-headed Woodpeckers was of immediate importance. How could one be sure that the same bird was in the same territory each week? Close observation indicated that individual Red-headed Woodpeckers may have natural markers. Three of the 12 woodpeckers, for example, were immature birds with black bars on their white primaries. The pattern of these bars varied among the individuals. Furthermore, one of these immature birds, even in the fall, had a red head and a black back whereas the other two were dull and brownish until the following April. The nine remaining woodpeckers had adult plumage but each had traits of behavior which became recognizable on prolonged observation. RH-5, for example, bowed incessantly, whereas RH-2 would swing in and out of its roost hole many times before entering at dusk. Of more general value in recognition was the fact that each Red-headed Woodpecker had certain resting places,

as well as anvils for pounding acorns, to which it would return on repeated occasions.

(B) Each Red-headed Woodpecker had a roost hole within its territory and would, with few exceptions, return to it on successive nights. I made my most prolonged observations on RH-2. This woodpecker entered its roost hole, which was 15 feet from the ground in a dead locust stub, at 5:10 p.m. on November 11, 1956. The bird remained inside as the sun set. At 4:45 p.m. on November 24 it disappeared in the same roost hole. On two other dates, December 22, 1956, and May 2, 1957, I watched RH-2 fly from its roost hole as the woods grew lighter after dawn. Thus one Red-headed Woodpecker used the same roost hole for six months.

FIG. 2. Creek Wood, as seen from south corner looking northward (Territory RH-5, Fig. 1).

(C) Observations on individual Red-headed Woodpeckers indicated that they usually flew only short distances, for such purposes as carrying an acorn from one tree and re-storing it in another or taking it to an "anvil" to break it in pieces. One could learn much concerning which trees were within the territory of any one individual by noting the extremes of such flights. Dividing lines between territories were, for the most part, sharp and definite. RH-9 not infrequently flew straight down along its northern boundary without disturbing its neighbor, RH-3, which might be only a short distance on the other side. RH-5 and RH-11 visited the same black walnut (*Juglans nigra*) to get sap from sapsucker holes. The two woodpeckers might cling to different branches only 10 feet apart, each returning, on separate occasions, to the same group of holes. This peaceful behavior was noteworthy, for any trespass of one Red-headed Woodpecker onto the territory of another usually led to considerable commotion.

(D) Territorial conflicts between Red-headed Woodpeckers were rare. When they did occur, however, one wondered if all of the Red-headed Woodpeckers in Creek Wood didn't join in with excited "quirrs" even though only a few of them were immediately involved. On December 16, 1956, for example, I saw a flash of black and white as one of the woodpeckers suddenly flew the length of the wood. This Red-headed Woodpecker on the loose flew over the territories of RH-12, RH-9, and of RH-2 (Fig. 1). Each of these latter woodpeckers attacked the intruder in succession as it passed over their respective boundaries, affording in the attacks an impressive demonstration of territoriality.

(E) Conflicts between Red-headed Woodpeckers and titmice or Downy Woodpeckers were common and gave more frequent demonstrations of boundaries than the intraspecific conflicts described above. On December 16, 1956, I was standing on the boundary between territories of RH-3 and RH-9 when the latter woodpecker flew up to within 20 feet of me as it drove some titmice from its territory. The titmice now excited RH-3, which flew down from a distant perch to attack the invaders in its turn. When the titmice, continuing on their passage through the wood, crossed into RH-2's territory, they were attacked for a third time. Thus I had watched three Red-headed Woodpeckers defending their territories in an aggressive fashion. All carried their attacks on the titmice up to but not beyond their respective boundaries.

Downy Woodpeckers usually passed through Creek Wood singly and were not easily driven away. I even came to think that one of them had become adjusted to repeated attacks.

On December 22, for example, I was standing on the boundary between the territories of RH-2 and RH-9 when RH-2 swooped at the Downy Woodpecker three or four times, almost hitting it. The smaller woodpecker, however, dodged around its tree trunk and continued hammering. It finally flew to an ash tree above my head. RH-2 pursued it but, seeing me, stopped at a distance and began to "quirr." RH-9 now approached from the opposite side. I was now in between two Red-headed Woodpeckers with the Downy Woodpecker above me. The way the Red-headed Woodpeckers kept bowing their heads and clinging to awkward perches suggested that both were disturbed by the presence of the smaller woodpecker. The Red-headed Woodpeckers never paid any similar attention to my presence alone. Another episode took place two days later. The Downy Woodpecker again came to rest over my head after being chased in succession by RH-12, RH-11, and RH-5. I was standing on the edge of RH-8's territory. This Red-headed Woodpecker was obviously excited but it appeared afraid to come closer. The Downy Woodpecker now worked above me, undisturbed for 15 minutes. It was attacked immediately when it flew away. I wondered whether the Downy Woodpecker in a trial and error process had found that the area above my head afforded a temporary refuge.

(F) A fresh fall of snow in January afforded an opportunity to verify the boundaries which I had sought to establish by the various methods described above. By tramping trails around each conjectured territory I was able to convert Creek Wood into a map not unlike Figure 1. Conditions were

ideal for observation. The Red-headed Woodpeckers, with their striking color patterns and resounding "quirrs" flew back and forth in the gamut of their activities against a background of bare trees and white snow. The boundaries were much as on previous days, but I was able to map out more sectors. Some few zones where little happened were difficult to determine. Figure 1 represents the situation in a general way and shows that the Red-headed Woodpeckers were crowded together in relatively small territories. Larger territories may not have been desirable from a woodpecker's point of view for they would be more difficult to defend. Another consideration was that territories had vertical as well as horizontal dimensions, and an abundance of dead locust trees with rotted-out centers providing storage space may have been of greater importance than mere area. The three immature woodpeckers, RH-1, RH-4, and RH-10 (Fig. 1) appeared to occupy the least desirable territories. Those of RH-4 and of RH-10 were especially large as well as being relatively devoid of dead trees. One might speculate that experienced adults would occupy smaller, more defensible areas if the trees were suitable. It was of interest from this point of view that nearly all the adult Red-headed Woodpeckers in Creek Wood were bunched in territories east of the creek where the dead locusts were located. Locations of roost holes gave corroborative evidence of this situation. All the Red-headed Woodpeckers, for example, which inhabited the easternmost territories, roosted in locust stubs (RH-2, RH-3, RH-5, RH-8, RH-9, RH-11, and RH-12; Fig. 1). The remaining five woodpeckers, of which three were immature birds, occupied the western portion of Creek Wood. Here four roosted in dead elms and the fifth in a black walnut.

Exceptional Territorial Behavior

A remarkable feature of the Red-headed Woodpeckers in Creek Wood was that they almost never left its borders while in residence. RH-1 and RH-10, both immature, would make occasional sorties to catch insects in an adjacent field in favorable weather. RH-4, also an immature bird, was the most exceptional of the Red-headed Woodpeckers in regard to wandering, as I first discovered on November 24, 1956, when I could not find it in its territory by the roadside. The woodpecker was still missing a week later. A constant succession of birds of various species were coming to plunder the stores of acorns which RH-4 had hammered into crevices of a dead elm. The elm came to resemble a large feeding tray. Titmice were the most frequent visitors but, to my surprise, White-throated Sparrows (*Zonotrichia albicollis*) came up at dusk to feed on bits of acorn. Two Red-bellied Woodpeckers made repeated visits to remove acorns, occasionally encountering a Red-headed Woodpecker, RH-7, which would drive them away. RH-7 also took acorns but showed no

disposition to take over any of the vacated, neighboring territory. This was an example of the conservatism of the Red-headed Woodpeckers, none of which, as far as I could observe, ever changed its boundaries once these had become established. RH-4, the wanderer, suddenly reappeared after an absence of two weeks. It remained in Creek Wood until early spring, apparently compensating for its lost acorn stores by flying out after insects whenever possible.

Spring and Departure

The Red-headed Woodpeckers showed few signs of a breeding urge until the season was well advanced. Whereas Red-bellied Woodpeckers were drumming, calling, and forming pairs by the end of January (Kilham, 1958c), March 24, 1957, was the first day on which I saw a Red-headed Woodpecker drumming. The drumming came in bursts of about one second's duration and was repeated two or three times. Many of the Red-headed Woodpeckers seemed never to drum and I presumed these were the females, since female Red-bellied Woodpeckers are known to drum rarely. Conversely, other individual Red-headed Woodpeckers, presumably males, drummed with increasing frequency.

On April 20 I heard a new note which I had not heard previously. This was a sharp "quee-ark." The calling of "quee-ark" and the drumming now became common. At the same time one observed that one woodpecker might fly into the territory of another and be tolerated. RH-6 did much calling and drumming. Since other woodpeckers seemed to come to his territory, rather than *vice versa*, I wondered if he were not a male and the visitors females. All the immature Red-headed Woodpeckers had assumed adult plumage by the latter part of April. With these various developments I began to wonder whether some of the Red-headed Woodpeckers might not stay to nest in Creek Wood. In spite of their new activities, however, the Red-headed Woodpeckers were still spending most of their time within their own territories, and even at the end of April continued to feed on their stored acorns. Their departure from Creek Wood came rather abruptly. On May 2 I could find only three Red-headed Woodpeckers and on May 5 I saw the last one. On that final day RH-6, still aggressive, drove away a Red-bellied Woodpecker.

Summer

Creek Wood seemed deserted after the departure of the Red-headed Woodpeckers. Toward the end of May, 1957, a pair of Red-bellied Woodpeckers had moved in and were obviously preparing to nest. I was away in June, but through July and August I made repeated visits to observe the Red-bellied Woodpeckers and the three young ones which they had raised. No Red-headed Woodpeckers were seen in these months, either in the wood or along

the canal. There was none on August 31, when I again searched through Creek Wood. On the following day, however, I caught a glint of sunlight on white. A Red-headed Woodpecker had returned. It appeared to be quiet and subdued and in following it about I observed an episode contrary to expected winter behavior. The Red-headed Woodpecker was clinging to a tree trunk when it suddenly flattened against the bark with its bill pointed straight forward. I then noticed that a Downy Woodpecker had alighted two feet above it. The Red-headed Woodpecker remained "frozen." There was no attack and no "quirrs." I wondered whether it failed to act aggressively because, having just arrived, it had no established territory and no stored acorns.

Fluctuations of Red-headed Woodpecker Populations

A severe drought afflicted the Seneca area in the summer of 1957. The swamp became hard and dry and Creek Wood had a withered appearance. During September I saw a few Red-headed Woodpeckers by the canal but only the one came to Creek Wood and none remained elsewhere in places where I had found many the year before. The reasons why Red-headed Woodpeckers appeared, then moved on, can only be conjectured. Three explanations suggested themselves. First, Creek Wood and the swamp had no water and I had observed that the woodpeckers of previous seasons came down to drink not infrequently. Second, there was a scarcity of insect life during the drought. A possible indication of this, apart from direct observation, was that the fall warbler migration in the area was unusually poor. Finally, the pin oak acorn crop was minimal. One could see this by scanning the trees or by noting that far fewer Blue Jays came for acorns than in the previous year. The winter season of 1953–54 offered an interesting comparison. The entire pin oak acorn crop failed in 1953 and not a single Red-headed Woodpecker wintered in the Seneca area as far as I could determine.

A Lone Wintering Red-headed Woodpecker

During the winter of 1957–58 I knew of only one Red-headed Woodpecker in bottomlands along the Potomac. This lone woodpecker lived in the center of Creek Wood. It gathered acorns while such were available and I watched it seal in its stores with slivers of damp, rotten wood, usually taken from dead limbs of adjacent live pin oaks. The winter was unusually cold, with much snow. There seemed to be no warm days with insects flying about. How could the lone Red-headed Woodpecker survive under such adverse circumstances? The bird was not at a loss. From November to March I watched it make repeated flights to a cornfield 400 yards away. It would devour some kernels by pounding them on trees adjacent to the field but it carried

others in its bill when, with a direct and undulating flight, it flew back to Creek Wood.

The behavior of this single Red-headed Woodpecker differed in several respects from what I had observed the year before when numbers of the same species had lived in a community. For one thing I almost never heard the single woodpecker call "quirr." Secondly, the area occupied by the Red-headed Woodpecker could not be called a territory, by one interpretation of the word, for, in the absence of close competitors of its own species, the lone woodpecker seemed to recognize no definite boundaries to its movements. It did, nonetheless, spend most of its time within a small circle of trees. The lone Red-headed Woodpecker would occasionally drive away a Red-bellied Woodpecker and less frequently a Downy Woodpecker or a Tufted Titmouse.

Discussion

The term territory is used in this report in reference to relatively small areas with well-defined boundaries, which included stores of large numbers of acorns and were defended by the notably aggressive behavior of their owners, the Red-headed Woodpeckers. I have not read of any closely similar type of territory, based on food storage, among other birds. I have, however, observed two situations where mammals established individual territories in late summer in a manner not unlike that described above for Red-headed Woodpeckers.

In one case Red Squirrels (*Tamiasciurus hudsonicus*) were harvesting pine cones (*Pinus strobus*) in Tamworth, New Hampshire (Kilham, 1954), in a section of pine woods clear of undergrowth. Repeated observations made early in September indicated that an individual squirrel had a definite territory and would sometimes run around its actual boundary. The animal was transporting cones to caches near the center of its domain. It appeared to warn off neighboring squirrels, engaged in similar activities, by means of its loud, chattery song, and conflicts between squirrels, in which the defending animal was dominant, were not infrequent.

In a second situation, Pikas (*Ochotona princeps*) inhabiting an open rock slide in mountains in Montana were observed over a period of four weeks (Kilham, 1958*a*) harvesting sprigs of vegetation which they accumulated in piles above and under the rocks. Each Pika maintained a definite territory which it would defend against neighboring Pikas and advertise with a frequently uttered "caack." These animals live on stored food while active under the snow in winter.

The Red-headed Woodpeckers, Red Squirrels, and Pikas had some features of strategy in common. All had small, readily defended territories surrounded by similar territories of others of their own species. Furthermore all three species were noisy. Their calls may have been warnings which served to diminish interspecific conflicts. In one sense the Pikas differed from the other two species for they stored miscellaneous types of vegetation that would have been available almost any year. The Red-headed Woodpeckers with

their acorns and the Red Squirrels with the pine cones, on the other hand, were taking advantage of bumper crops, such as might be entirely absent in other years. One might think of the last two species as being mobile opportunists.

Winter territories have been described for other birds. Lack (1943) states that the British Robin (*Erithacus rubecula*) may establish an individual territory in the autumn which it uses as a foraging area. Unrelated food competitors are not driven away. The situation observed among the Red-headed Woodpeckers was different in that they might collect acorns outside of their territories if they had no suitable pin oaks within them (Kilham, 1958*b*). The woodpeckers drove away all avian competitors, related or not. A Mockingbird (*Mimus polyglottos*) exhibited a somewhat parallel behavior when it took to defending a group of persimmon trees opposite Creek Wood. On November 25, 1956, it drove away a Yellow-bellied Sapsucker, then a Downy Woodpecker, which had come to feed on persimmons.

The Greater Spotted Woodpecker (*Dendrocopos major*) is reported by Pynnönen (1939) to live mainly on pine and spruce seeds in Finland in winter. Individuals hold territories with distinct boundaries, although food apparently is not stored within them in significant amounts. These territories, apparently ranging from 2½ to 8 acres in extent, were large in comparison to those described above for Red-headed Woodpeckers.

Swanberg (1956) describes food storage as one of the main functions of territories held the year around by Thick-billed Nutcrackers (*Nucifraga caryocatactes*) in Sweden, the winter stores of nuts being used to feed the young in spring. Such territories averaged over 30 acres in extent. The Red-headed Woodpeckers described above, on the contrary, were migratory and had settled down into small winter territories where food supplies were optimal. Here they competed directly with Red-bellied Woodpeckers, both for food and habitat.

Summary

Twelve Red-headed Woodpeckers wintering in Maryland were observed to maintain small, individual territories over eight months in 1956 and 1957. The Red-headed Woodpeckers defended their stores of pin oak acorns against other birds, both related and unrelated, and appeared to be the most aggressive of the local species of woodpeckers. Conflicts with such birds as Tufted Titmice enabled one to mark the boundaries of the woodpeckers' territories with some precision. Each Red-headed Woodpecker had a roost hole within its territory. Calls and drumming expressive of a breeding urge did not become prominent until April. The woodpeckers had all departed by the first week in May. The pin oak crop was minimal in the fall of 1957, and

under these circumstances only a single Red-headed Woodpecker returned to winter. This bird subsisted largely on corn from an adjacent field. Although it spent most of its time within a small circle of trees the lone woodpecker had no discernible territorial boundaries in the absence of neighbors of its own species.

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DISPERSAL OF EGRETS ON THE KANTO PLAIN, JAPAN

BY H. ELLIOTT McCLURE

DURING the period 1949 through 1957 the relationship between wild birds and Japanese Encephalitis was under study at the U.S. Army 406th Medical General Laboratory, located at Tokyo, Japan. The avifauna of the Kanto Plain which surrounds Tokyo is not extensive in numbers of individuals or in species (McClure, 1957. *Wilson Bull.*, 69:323–332), but a survey of blood sera made in 1950–51 (Hammon, Sather and McClure, 1958. *Amer. Jour. Hyg.*, 67:118–133) showed that infection with this virus was widespread among birds. Concentrated study at two ardeid breeding colonies from 1952 to 1957 resulted in isolation of the virus from both birds and mosquitoes. The objective of this study was not to incriminate ardeids as the reservoirs of the disease, but to use them as pilot indicators of what may happen among many species. Ardeids are large and were easy to obtain in sufficient numbers to yield adequate data for summarization.

Virus encephalitis is a disease attacking birds, livestock, and human beings in late summer with the peak of virus dissemination among mosquitoes occurring in late July and early August. When a susceptible bird becomes infected the virus circulates in the blood for a period as long as a week. The possible role that birds might play both in the dissemination of the virus from foci of infection and its seeding among mosquitoes was brought under consideration. This obviously is a very difficult field problem to solve without extensive banding and wide recapture of species susceptible to the disease and large enough to be bled repeatedly of proportionately large volumes of blood (1 to 3 cc.). The rate and degree of dispersal of juveniles of any species over the Kanto Plain was not known. As egrets were large, conspicuous, and easily seen from the air, the present study was designed in order to accumulate information concerning changes in the population of egrets over the Kanto Plain, and to infer therefrom the rate of dispersal of juveniles and their penetration into little-used areas. Egret as used herein refers only to the members of the genus *Egretta* observed during the study.

Locale and Methods

The Kanto Plain (Figs. 1 and 2) lies to the north and west of Tokyo, an extensive alluvial plain drained by three river systems, the Tonegawa (largest and northernmost), Arakawa, and Tamagawa. Its level rice fields are broken only occasionally by low hills. To the east and north of Tokyo is a region of low, flat-topped hills (which extend down the Chiba Peninsula), interspersed by narrow level valleys along the watersheds. This upland gives way on the Pacific Coast to a coastal plain also cultivated in rice. The uplands

support second-growth deciduous and evergreen forests and fields of truck crops, whereas all lowlands are planted in rice, except the small areas about each village or farm home which are in gardens or shade trees.

Weather permitting, at the middle of each month, from January, 1955, through December, 1956, an aerial survey was made along a route (Fig. 1), beginning at Tokyo and extending north to Sagiyama, Kawagoe, Kumagaya, Camp Drew; along the Tonegawa to Katori; across Chiba Hills to the Pacific Coast; south to Katakai; back north and west to Imba-numa Lake; south to Chiba City; and thence west along the shore of Tokyo Bay over Shin Hama heronry to Tokyo. The 250-mile trip in an H 13 helicopter provided by the U.S. Army Air Force required five hours, and was always followed in the same direction, at the same time (9:00 a.m. to 2:00 p.m.), and at a height of about 500 feet. The H 13 is a two-place reconnaissance helicopter provided with a plexiglass cabin permitting observation in all directions but to the rear.

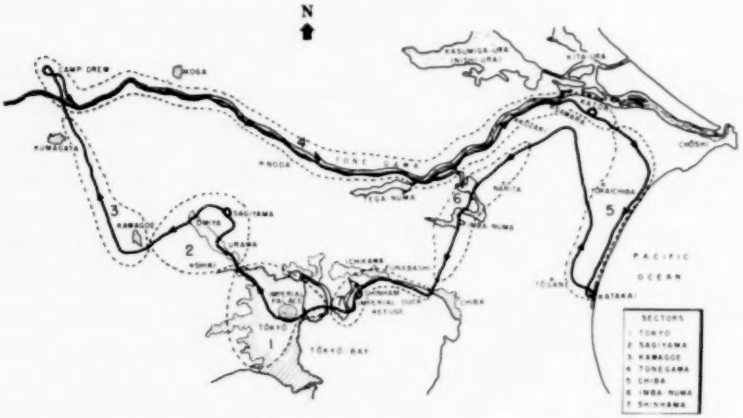

FIG. 1. Map of the Kanto Plain, Honshu, Japan, showing route of flight taken during monthly surveys of egret populations in 1955 and 1956.

It was found by experimentation that 500 feet altitude was about optimum for observation of egrets to one-half mile on either side. Below this height the egrets flushed readily but could not be seen over so wide an area, and above this height they did not flush and many were not seen. At nesting colonies (heronries) the location was circled, estimates were made of the number of birds visible, and photographs were taken. Later, the photographs were enlarged, examined under a dissecting microscope, and the birds were counted. Actual numbers in all other flocks were tallied and recorded on large maps at the points where they were seen.

From January, 1951, through December, 1954, regular bird tallies, varying from once a week to once a month, were made by walking through selected habitats near Tokyo. These included rice lands and tide flats similar to those shown in Fig. 3, as well as the heronry at the Shin Hama Imperial Duck Netting Grounds. Observations were made from blinds about the central pond, and in 1956 an attempt was made to count all of the nests present.

At the Sagiyama heronry, located among farmyard trees about 10 miles north of Tokyo, the population was estimated from nest counts in 1956 and 1957.

Colonies and *heronries* are used here as synonyms indicating permanent locations of herons or egrets; they indicate roosting in the winter, or roosting and nesting in the summer. The route of flight crossed three such heronries, an immense nesting colony at Sagiyama and a smaller one at Katori (neither used in winter), and the large heronry at Shin Hama which was used the year around.

Results and Discussion

Before the concentrated studies of 1955, 1956, and 1957 large numbers of ardeids were recorded: Grey Heron (*Ardea cinerea*), 1025; Great Egret (*Egretta alba*), 635; Plumed Egret (*E. intermedia*), 22,500; Little Egret (*E. garzetta*), 45,000; Cattle Egret (*Bubulcus ibis*), 400; Black-crowned Night Heron (*Nycticorax nycticorax*), 52,500. These figures represent the

Fig. 2. The Kanto Plain near Tokyo in early summer.

totals from tallies on the ground. From the air no attempt was made to distinguish species of egrets, and only few herons were noted. The total egrets recorded from the air was 45,225. During 1956 the count of nests at Shin Hama placed the breeding pairs at about 400 Night Herons, 250 Little Egrets, 130 Plumed Egrets, 5 Great Egrets, and 5 Cattle Egrets. A nest count at the Sagiyama colony in 1957 placed the breeding pairs at about 700 Great Egrets, 1,000 Black-crowned Night Herons, 1,400 Plumed Egrets, 250 Little Egrets and 50 Cattle Egrets.

Although *Nycticorax* is as abundant as the Little or Plumed Egrets at the colonies it is nocturnal and none was seen in the aerial studies. The Grey Heron was seen predominately as a winter resident at Shin Hama and along the tide flats of Tokyo Bay. The only nesting colony found was in tall *Cryptomeria* trees at the Katori Shrine. This colony was too distant from the laboratory for study.

TABLE 1

THE SPECIES COMPOSITION OF EGRETS AND HERONS IN THE TOKYO AREA, 1951–1954, AS INDICATED BY THE PERCENTAGE OF THE POPULATION MADE UP OF EACH SPECIES EACH MONTH

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Birds seen outside of nesting colonies												
Little Egret	67.1	87.0	95.3	76.6	54.4	52.5	47.7	51.5	54.2	73.4	90.2	87.5
Plumed Egret			1.3	11.3	31.8	37.8	40.6	24.8	33.7	14.7		
Great Egret		3.0			2.7	1.2	4.7	1.2	3.2	2.4		1.6
Cattle Egret												
Grey Heron		3.0	.3	.8				2.3	2.3	.5	4.3	.4
Night Heron	32.8	6.8	2.9	11.1	10.9	8.3	6.8	19.9	6.3	8.8	5.4	10.3
Birds seen at the colony site, Shin Hama												
Little Egret	35.9	37.4	44.8	49.3	43.1	33.1	39.0	37.2	33.5	5.1	9.7	1.2
Plumed Egret				3.5	18.7	25.4	24.2	34.9	28.1	1.2	.1	
Great Egret	.2	.2	.1	.3	.8	.4	.1	.2			.9	.3
Cattle Egret					.5	.6	.4	.4				
Grey Heron	3.3	3.9	.7	.1				.1	.5	18.0	5.6	3.4
Night Heron	60.3	58.3	54.1	46.5	36.7	40.2	35.9	26.9	37.5	75.0	83.4	94.8

During the period from 1951 through 1954, when regular tallies were being made, the Shin Hama colony was undisturbed and the species composition was that shown in Table 1. By 1954 the concentration of birds was great enough that protective bamboo surrounding the ponds was being killed by the birds' feces. Shin Hama is an Imperial Duck Refuge and netting grounds so the refuge attendants began shooting the ardeids to drive them away. They continued this practice intermittently every year. The Plumed, Great and Cattle egrets are more wary than the Little Egret or the Night Heron; therefore the species composition changed rapidly and the 1956 nest tally showed a great reduction in all but the latter two species.

No studies were made at Sagiyama before the 1955–56 aerial observations, but the nest tally in 1957 showed the species composition as reported in a previous paragraph. Here the colony has been a National Preserve for more than 300 years and is probably more stable than that at Shin Hama. The loss of trees is not a problem since the guano is harvested each year.

In rice fields and on tide flats the species composition of diurnal ardeids is very different from that at the colonies. The Little Egret is a permanent resident and is the most abundant and conspicuous species at all seasons, whereas the Plumed Egret is a summer resident and reaches peak abundance in July and August. Great and Cattle egrets are seen in negligible numbers in the fields.

The annual cycle of abundance as seen both away from and at colonies is shown in Table 2. There is a conspicuous difference in this cycle, for greatest

TABLE 2

SEASONAL OCCURRENCE OF ARDEIDS IN THE TOKYO AREA EXPRESSED AS THE PERCENTAGE OF THE ANNUAL TOTAL FOR EACH SPECIES

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Birds seen outside of nesting colonies												
Little Egret	.6	2.8	6.9	5.5	3.0	5.1	10.0	23.1	25.0	9.2	3.1	5.1
Plumed Egret		.2	1.8	4.0	8.5	19.6	25.6	35.7	4.2			
Great Egret		2.6			3.9	3.2	26.1	14.7	38.5	8.1		2.6
Cattle Egret												
Grey Heron		3.8	.9	2.4				41.0	42.5	2.4	5.7	.9
Night Heron	6.5	1.1	1.1	4.2	3.1	4.3	7.5	46.7	15.3	5.7	.9	3.2
Birds seen at the colony site, Shin Hama												
Little Egret	5.6	5.7	5.8	18.0	13.7	14.8	20.0	10.7	4.0	.1	.7	.1
Plumed Egret				2.9	13.3	25.4	27.8	22.6	7.6			
Great Egret	3.9	3.0	1.9	13.5	27.4	20.8	9.8	7.6	.4	.2	7.0	3.9
Cattle Egret					19.8	35.7	30.1	14.2				
Grey Heron	19.9	22.6	3.7	1.6	.1	.4	.3	1.4	2.6	17.2	15.2	14.4
Night Heron	7.8	7.3	5.8	13.9	9.6	14.7	15.1	6.4	3.7	1.5	4.9	8.6
Total egrets seen only outside colonies from 1951–1954												
	.4	2.0	4.7	4.2	3.3	6.1	13.2	23.6	28.5	7.7	2.1	3.5
Total egrets seen only at Shin Hama from 1951–1954												
	3.4	3.9	4.0	13.3	13.7	18.2	22.4	14.4	5.1	.1	.5	.1
Total egrets seen from air outside colonies in 1955–1956												
	2.3	3.2	3.0	5.2	5.6	7.5	7.2	17.7	21.5	16.0	5.3	4.9
Total egrets seen from air at nesting colonies in 1955–1956												
				7.2	21.0	20.9	31.0	14.7	1.2			

numbers occurred in the colonies at the peak of nesting in June and July as contrasted with peak numbers in August and September away from the colonies.

One other facet as background for the 1955–56 aerial study had been explored in March, 1952. Each evening during winter approximately 1,000 Little Egrets return to Shin Hama to roost in the bamboo. An attempt was made to mark some with an alcohol-soluble red dye by spraying the dye over groups while they slept. Red-spotted individuals were seen feeding in rice fields as far away as four miles. That the daily range may be much more than this for some species was suggested by the fact that salt water fish were found in the diet of nestling Great Egrets at Sagiyama, more than 15 miles from Tokyo Bay.

The route of travel for the aerial survey was arbitrarily divided into the topographic sections shown in Fig. 1. These were as follows: (1) *Tokyo*, the city and its immediate environs. In the heart of the city at the Imperial Palace grounds there is a small colony of 50 to 100 pairs of ardeids. Since this area was "Off Limits" to all but the Imperial Household no study was made, but seasonal observations of the locality indicated that most of the egrets were the Plumed Egret, and that the Black-crowned Night Heron

made use of it the year around. Evening flights of egrets from, and Night Herons to, rice fields south and west of the city were noted regularly. (2) *Sagiyama.* This sector included extensive rice fields broken by occasional uplands cultivated in truck crops. The route passed over the Sagiyama heronry already described. Also, within this sector was a small nesting colony at Shiki. This location was in use only in the summer and provided nest sites in dense bamboo for the Little, Plumed and Cattle egrets and the Night Heron. No attempt was made to tally breeding birds. (3) *Kawagoe.* From the village of Kawagoe north to the Tone River the route passed over broken hills with rice cultivation along the watersheds. Here there were no colonies known to the author.

FIG. 3. Shin Hama Imperial Duck Netting Grounds in late summer after the egrets have dispersed. Tokyo Bay is at the left.

(4) *Tonegawa.* Except for isolated hills the Tone River is bordered with extensive rice fields. The location of a nesting colony near Camp Drew was suspected from actions of the egrets, but was not learned. The colony at Katori has already been described. It was used only as a nesting site by the Grey Heron, Night Heron, Great and Plumed egrets. (5) *Chiba.* This sector included the coastal plain under rice and grain cultivation. No colony was known here. (6) *Imba-numa.* Between the Chiba and Imba-numa sectors the route crossed low hills interspersed with narrow rice-cultivated valleys, in which egrets were not noted during the surveys. There were no heronries known to be near Lake Imba-numa and birds using this marsh and lake apparently flew in from Shin Hama. (7) *Shin Hama.* This sector included the tide flats along the north shore of Tokyo Bay and the rice fields around the Shin Hama heronry as well as the colony itself.

Weather conditions, season, vegetation, and topography affect the visibility of egrets, but experienced pilots placed the average range at which the birds could be seen at one-half mile on either side of the helicopter at 500 feet altitude. Using this factor and the linear distance over which the plane traveled, a fairly accurate population per square mile could be estimated. Since the birds were almost never seen in any habitats but rice fields or tide flats, the percentage of the land in rice was used to reduce the figures to the number of birds per square mile of paddy.

The results of 24 months of aerial observation are summarized in Tables 3 and 4 and illustrated in Figs. 4 and 5. The seasonal pattern was fairly distinct. From January through March the winter population was stable, averaging about 2.7 Little Egrets per square mile of paddy. They frequented the fields that did not freeze over. Flocks of Plumed Egrets and others began

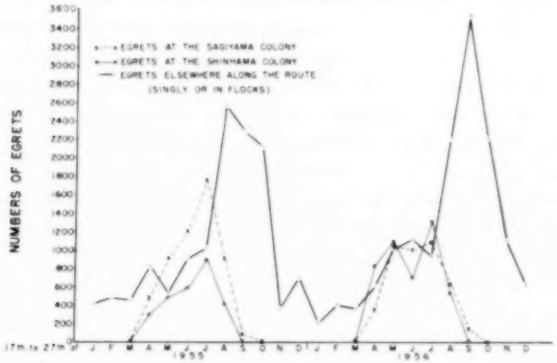
NUMBERS OF EGRETS
EGRETS AT THE SAGIYAMA COLONY
EGRETS AT THE SHINHAMA COLONY
EGRETS ELSEWHERE ALONG THE ROUTE (SINGLY OR IN FLOCKS)
1955
1956

FIG. 4. Numbers of egrets counted along a 250-mile route on the Kanto Plain of Japan.

TABLE 3

AVERAGE NUMBER OF EGRETS ESTIMATED PER SQUARE MILE ON THE KANTO PLAIN

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Avg
					1955								
Average birds per square mile	1.6	1.9	1.8	3.2	2.1	3.6	4.0	10.2	9.0	8.4	1.4	2.7	4.2
Total birds tallied outside colonies	417	478	452	817	528	913	1018	2571	2273	2105	361	693	
Total birds tallied at colonies				732	1563	1926	2880	1440	77				
					1956								
Average birds per square mile	.84	1.6	1.5	2.3	4.0	4.4	3.6	8.7	14.0	8.7	4.2	2.5	4.7
Total birds tallied outside colonies	212	401	373	592	1001	1105	920	2187	3522	2201	1069	634	
Total birds tallied at colonies				1270	2315	1924	2831	1273	145				
Two-year average number of egrets per square mile of rice field including birds at colonies	2.2	3.1	2.9	5.0	5.4	7.1	6.8	16.7	20.4	15.2	8.8	4.7	
Estimated total egrets in rice fields on Kanto Plain including those at colonies	2945	4119	3865	6611	7171	9464	9091	22327	27193	20208	11730	6225	

arriving from the south in April, and the population per square mile nearly doubled. During the period from May to July heronries were occupied and the population density in paddies showed a slight increase. More than 50 per cent of all egrets counted in the fields were seen there during August, September, and October when juveniles left the heronries and the population density rose to 17.4 birds per square mile. Migration rapidly depleted the population so that the November density was equivalent to that of April. In December the population consisted only of Little Egrets, again dispersing to flooded, unfrozen paddies, marshes, and tide flats. This population trend from month to month is illustrated in Fig. 4, wherein the total number of egrets counted in rice fields is compared with those seen at Sagiyama and Shin Hama heronries. This figure suggests that the influx of egrets on the Kanto Plain in late summer is the result of production of young at colonies and the cessation of nesting activities by the adults. It is known that heronries are present in Japan north of the Kanto Plain, but that very few egrets remain north of the plain over winter. Therefore, part of the fall population of the plain is made up of migrants from the north.

TABLE 4

SEASONAL USE OF RICE FIELDS IN THE KANTO PLAIN, JAPAN, BY EGRETS, EXCLUDING BIRDS COUNTED AT NESTING COLONIES

Months	Egrets counted per square mile of paddy		Percentage of total egrets for the year	Remarks
Jan.–Mar.	2.7		9.6	Overwintering flocks of Little Egrets
April	5.0		5.5	Immigration of all species
May–July	6.4		21.2	Nesting in heronries
Aug.–Oct.	17.4		53.4	Dispersal and migration
Nov.	5.0		5.3	Migration
Dec.	4.7		5.0	Little Egret movement on Kanto Plain
Average	7.9	Total	100.0	

The population density in the sectors and effects of dispersal are diagrammed in Fig. 5. Here it is evident that each sector receives maximum use at certain seasons. At Tokyo the population is negligible except for movements of residents to and from the Palace heronry. In the Sagiyama sector the activity at the Sagiyama and Shiki colonies produces a heavy and increasing population in the rice fields with the greatest density in August. This is followed by a rapid reduction as the birds disperse and migrate. The Kawagoe population reflects the activity at the Sagiyama and Shiki colonies. Because

of its limited rice acreage this sector was little used until July and August when juveniles were leaving the colonies. The same was true of the Tonegawa sector. Here the extensive paddies supported a low, uniform population until the late summer dispersal and the arrival of migrants in October. The pattern in the Chiba sector was different from that in the others. In winter the paddies rarely freeze and there is a wintering population that disappears during the nesting season. This situation was reflected in the aerial counts. During late summer dispersal birds moved back into the Chiba area and many remained there. The Imba-numa sector was one of winter usage. Very few birds were present except when other sources of food were dried up or frozen. The Shin Hama sector had a population density which reflected all the seasonal activities of the egrets. The presence of tide flats, paddies and the heronry made the area attractive to egrets, and the population density was high all year. Peak numbers were reached in October when the local and migrant birds concentrated there before leaving for the south.

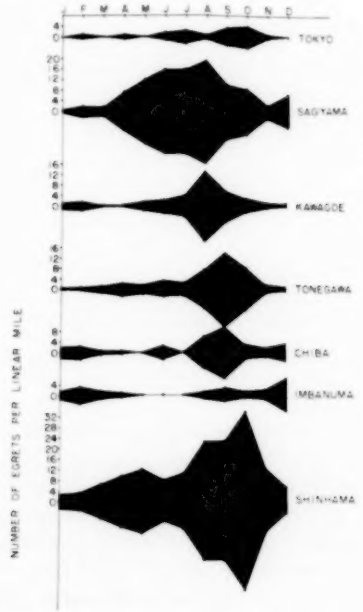

FIG. 5. Average numbers of egrets counted outside the colonies along each major division of the aerial survey route on the Kanto Plain. Data for the 24 monthly surveys, 1955–1956, are averaged.

These conclusions can be substantiated only by the field observations since no birds were banded north of the Kanto Plain, and of the 5,000 nestlings banded since 1951 on the Kanto Plain very few have been observed after fledging.

Japanese agricultural reports indicate that there are approximately 1,330 square miles of rice fields on the Kanto Plain. Assuming that the survey route intercepted a representative sample of the population, the total population on the plain would fall within the vicinity of the values given in Table 3.

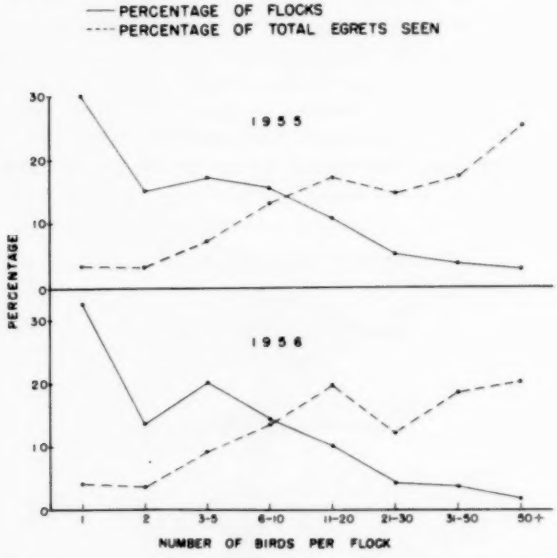

FIG. 6. The relationship between flock size and number of flocks of egrets on the Kanto Plain outside the colonies.

The determination of the number of young produced at Sagiyama or Shin Hama proved very difficult. Even though concentrated studies were made in 1952, 1953, 1956, and 1957, the number of broods reared or the number of nesting attempts per pair were not determined because of the difficulty of marking and/or identifying adults. The period of time that a nest is in use is about two months, and there is nesting at the heronries for five months. Weekly nest tallies at Sagiyama in 1957 indicated a total of at least 6,000 nests of *all species* from which an average of two young were produced, a total of 12,000 young. At the peak of nesting activity there were more than 3,000 pairs (3,029 by actual count), so that a total of 6,000 adults plus

12,000 young indicates at least 18,000 birds left this colony in August and September. Probably one-third of that number was at Shin Hama (the 1956 estimate was 6,500) and an unknown production at other colonies. Approximately one-third of this total were Night Herons which were not visible from the air. The estimated Peak number of 27,000 egrets on the Kanto Plain in September could have represented birds that originated locally.

An objective of the aerial survey of egret numbers was to determine if the simple visual dispersal of egrets over the plain correlated with the time of maximum virus infection, and if it was of such a nature that spread of the

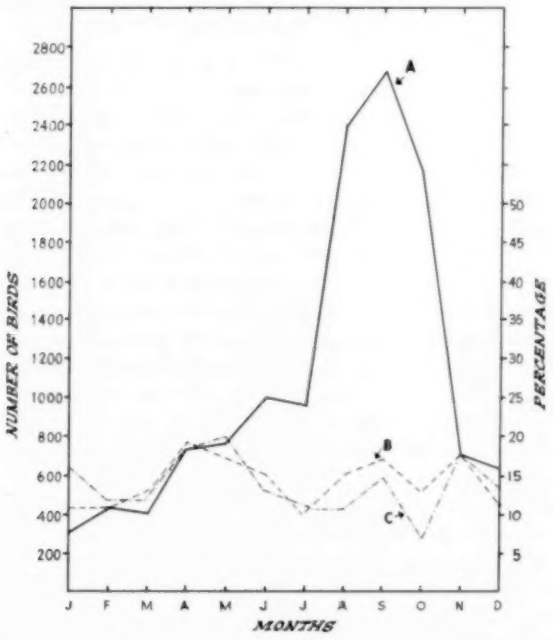

FIG. 7. Comparison of flock size to total population of egrets. A—Number of birds. B—Percentage of the flocks consisting of 6 to 10 birds. C—Percentage of the egrets tallied in flocks of 6 to 10 birds.

disease could be correlated with or inferred from the spread of infected juveniles. It does not follow that the simple increase as indicated by Fig. 4 would illustrate dispersal. That the dispersal was widespread and involved normally unused habitats was more clearly demonstrated when the data were summarized as shown in Fig. 5. There was one other pattern of the popula-

tion dispersal which demonstrated the infiltration into the available habitat, that of flock sizes.

The number and location of each group of birds was noted on maps and these groups or flocks were arbitrarily arranged according to the following sizes: individuals, pairs, flocks of 3 to 5, 6 to 10, 11 to 20, 21 to 30, 31 to 50, and more than 50 birds. The percentage of the flocks in these size categories and the percentage of the population in such flocks are plotted in Fig. 6, and the resulting comparison indicates that a flock size of around 6 to 10 birds was optimum. If this is true then it would be expected that the greater the population of egrets the more small flocks there would be and, by inference, the greater the penetration of the area. In flying over these flocks the birds were recorded as in a single flock if they were in close association, i.e. scattered over one field but at a distance from a similarly dispersed group. If the population were greater there should have been more fields with flocks in them, providing the ratio of large and small flocks were the same. This appeared to be true. In January, when the population was at low ebb, 11.4 per cent of the birds were seen in flocks of 6 to 10 as compared with 1.1 per cent of the birds in flocks of more than 50. These two categories made up 16.1 and 15.5 per cent of the population, respectively. In the peak month of September 17.5 per cent of the flocks were still in the 6 to 10 size category and 1.4 in flocks of more than 50. However, 15.3 per cent of the population was in the flocks of 6 to 10 and 17.3 per cent in the flocks of more than 50. Fig. 7 illustrates this for flocks of 6 to 10 individuals. Since the actual September population density was nearly 10 times that of January this means that there were nearly 10 times as many flocks and that the birds were dispersed over the available habitat rather than concentrated locally, possibly 10 times as widely dispersed.

This study, therefore, demonstrated these facts: (1) in this one group of birds, the ardeids, the population dispersal coincided with the period of maximum virus infection of the mosquito vector; (2) the dispersal was widespread over the Kanto Plain; (3) little-used habitats came into occupancy during this period; (4) and this penetration was fairly uniform since flock sizes did not increase with increased population density. It remains to be demonstrated that this dispersal pattern among single or many species of wild birds is or is not a factor in the dissemination of Japanese encephalitis virus and the seeding of the vector mosquito, *Culex tritaeniorhynchus*.

Summary

Between January, 1955, and January, 1957, 24 monthly aerial surveys of egret populations were made along a 250-mile route through the Kanto Plain, Japan, from a helicopter flying at 500 feet altitude. The objective of the

study was to learn if dispersal of juvenile egrets was correlated with the dissemination and infection of Japanese encephalitis virus in the Tokyo area. The following information resulted:

1. The egret population on the Kanto Plain in winter is low and composed mainly of Little Egrets (*Egretta garzetta*).

2. In April Plumed (*E. intermedia*) and other species of egrets arrive from the south and seek nesting locations or heronries.

3. The peak population in the heronries occurs in July and August.

4. Rapid dispersal of young from the colonies brings peak density over the plain in August and September when the population is 10-fold that of January.

5. Migration in October rapidly depletes the population.

6. Dispersal over the plain in late summer is widespread, and unused rice fields are sought out.

7. Flock size remains the same with wider habitat usage accommodating the increase in population.

8. In this one group of species the dispersal of young coincides with the peak of virus infection and dissemination among vector mosquitoes and mammalian hosts.

406TH MEDICAL GENERAL LABORATORY, APO 343, SAN FRANCISCO, CALIFORNIA, NOVEMBER 15, 1957 (Present address: U.S. Army Medical Research Unit, Institute for Medical Research, Kuala Lumpur, Malaya)

NOTES ON THE ECOLOGY OF *DACTYLORTYX THORACICUS*

BY EUGENE A. LeFEBVRE AND JOYCE HECKENLAIBLE LeFEBVRE

THE following notes on the life history and ecology of the Singing Quail (*Dactylortyx thoracicus*) are offered as a supplement to the comprehensive paper by Warner and Harrell (1957). Our studies, which were confined to one population, were conducted in the oak–sweet gum cloud forest (Fig. 1) on the Rancho del Cielo, owned by W. Frank Harrison and situated about five miles northwest of Gómez Farías in southwestern Tamaulipas, Mexico. This area, its geology, climatology, and vegetational characteristics have been described thoroughly by Harrell (1951 MS) and Martin (1958). In 1951, lumbering operations were begun in the area and the floristic and ecologic conditions were altered; most noticeable has been the general opening of the forest crown followed by a more dense growth of the understory (Figs. 2 and 3). We stayed in the field from April through June, 1953; and from April through July, 1954, J. LeFebvre again studied in this area. The following notes are a product of part of the studies made at these times.

ACKNOWLEDGMENTS

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HABITAT

Dactylortyx is found throughout the oak–sweet gum cloud forest at the Rancho del Cielo. Although, as Warner and Harrell (1957:125) point out, this species is regarded as a bird of the dense undergrowth, we found it common in the more open areas of the forest. However, there was some type of overhanging or screening vegetation in the areas where the quail were feeding, and an undergrowth was not distant from these feeding areas. Salvin and Godman (1897–1904:309) report finding quail at the edges of ravines in the mountainside forests where they "bask in open sunny spots."

To cite examples of the range of habitats utilized by the quail at Rancho del Cielo, a brief description follows. In several sections of the forest the quail occupy relatively undisturbed habitat which characteristically includes four layers: a small number of very tall oaks (*Quercus* spp.) and sweet gum (*Liquidambar styraciflua*) that provide an almost complete canopy; numer-

ous small and medium-sized oaks and sweet gum plus *Rhamnus caroliniana*, *Clethra macrophylla*, *Eugenia* spp. and *Ternstroemia* sp.; and shrubs and herbs common in the understory. The forest floor was thickly covered with leaf litter and mosses. In other regions of the forest, the canopy and secondary tree strata were similar to those described, but the ground cover was reduced, consisting only of a few scattered herbs. In those localities where most of the large oaks and sweet gum had been removed, a dense cover of pokeweed (*Phytolacca* sp.) and shrubby plants had invaded as an undercover

FIG. 1. (*left*) Relatively undisturbed area of oak–sweet gum cloud forest. FIG. 2. (*right*) Second-growth forest of partially lumbered area.

providing a changed habitat for the Singing Quail. Quail were observed frequently feeding on low-hanging pokeweed fruits. The pattern of the cutting operations in this locality left the cut-over areas greatly interdigitated with pockets, of varying sizes, of virgin or practically undisturbed timber. Most of the quail we observed in the disturbed habitat lived near the edges of these uncut areas, and certainly occupied sites which included both types of habitats. We observed quail feeding daily in the disturbed habitat and at all times of the day. This utilization of changed habitat agrees with the observations of Dickey and Van Rossem (1938:155), who found in El Salvador that the quail showed a decided tendency to favor the coffee groves instead of their natural oak scrub habitat.

We found no evidence of quail in certain areas within the oak–sweet gum cloud forest where the terrain was rocky and uneven and where there was little or no accumulation of soil or leaf litter among the moss-covered rocks. In these sites varying from one-quarter to three acres in extent, the vegetation did not differ markedly when compared to other sections of the forest.

Population Density

In the area comprising 20 acres enclosing and surrounding Mr. Harrison's ranch we located five pairs of quail in 1953 and four pairs in 1954. All except two pairs were found immediately adjacent to the ranch clearing. We estimated that elsewhere in the cut-over sections of the forest there was at least one pair of quail per 20 acres. Comparing these figures with the 3.5 pairs per 100 acres obtained by Harrell (1951 MS) in both 1950 and 1951 in the undisturbed forest, our estimate suggests a slight increase in the population in the changed habitat. Undoubtedly, these values are subject to error, but they indicate that in 1953 and 1954, the Singing Quail was maintaining its population density in the disturbed habitat.

Voice

The song of *Dactylortyx*, which has been described by Sutton and Pettingill (1942) and Warner and Harrell (1957:130), is both loud and musical. Most birds sang in the early morning and at dusk; however, the summer of 1953 was unusually dry and the amount of singing by this species as well as by other birds at the ranch was greatly reduced. On especially hot or dry days, no singing was heard at all, whereas cool, foggy or cloudy mornings prompted a few birds to sing. These observations agree with those of Sutton and Pettingill (1942).

In addition to the thrilling, thrush-like song, this species has at least two calls. One is a low-pitched, twittering call which we heard on almost all occasions when the birds were feeding. Often, too, when we came upon them in the forest, the quail would utter this call. Warner and Harrell (1957:130) suggest that this may be a location call for the family group. We had one particularly good observation of a bird giving this call when we flushed a pair of quail; the male landed 12 feet ahead of us on a rock and uttered the "twitter-call." We noted at that time, and on at least two other occasions, a peculiar quality in that this call often sounded like a duet with one voice just one note out of phase with the other.

The second call is a loud, sharp alarm whistle. We heard this only once in 1953, but it was recorded on several occasions in 1954, whenever the adults were accompanied by young. Once the alarm was issued, the adults would continue uttering the low "twitter-call," or on one occasion when we were examining the young, the parents clucked excitedly.

Behavior

Dactylortyx is primarily a bird of the forest floor and prefers to remain on the ground even when avoiding enemies. Although Warner and Harrell (1957:128) report no perching in this species, we have on four occasions seen them perching above the ground. In three cases when flushed or shot at, adult quail hopped onto nearby branches ranging in height from four to 12 feet. There they continued to twitter and began to bob their heads vigorously. When approached, these birds flew into nearby cover. In the fourth case, on May 7, E. LeFebvre observed a quail fly up onto a branch about 15 feet above the ground where it remained until darkness. This was the only case of arboreal retirement that we have noted.

Fig. 3. A recently lumbered area showing extent of removal of plant cover.

Some writers have stated that this species is wary, and that opportunity to observe it closely is seldom obtained. Our observations agree with those of Warner and Harrell (1957:7) in that *Dactylortyx* appears to be very tame at Rancho del Cielo. Certain pairs of quail became more wary, perhaps as a result of contact with people when lumbering activities began and transient workers moved into the region. The onset of the nesting season may also result in increased wariness. One pair of quail under almost daily observation showed little concern over our presence early in the study period, but several weeks later (about mid-June) it became increasingly difficult to approach this pair.

Care of Young

Behavior of the adults at the nest is not known, but both parents protect and care for the young once they have left the nest. On April 14, 1954, J. LeFebvre was alerted by

a sharp whistle given by a male standing at the side of a path. When it was approached, all bedlam broke loose. The female appeared, clucked very excitedly, and feigned injury by scurrying about with short, rapid steps and drooping wings. Both adults began to circle at a distance not more than five feet from the observer; meanwhile two young had scooted into a partly hollowed tree stump. They were found close together, heads hidden, and tails pointed upward and out. While one young was examined and replaced, the other one disappeared. The adult male tried to attract attention away from the young by calling and scurrying about. J. LeFebvre sat down about 20 feet away from the stump but both parents remained excited. Later the observer retreated further and the female flew onto a limb five feet about the ground, where she twisted, turned and clucked continually. The male had disappeared by this time and was no longer calling. Once the observer was hidden from view, the female stopped calling, hopped down from her perch and ran over to where the young had first been seen; the male came back to the stump, clucked once and disappeared. When the stump was examined, the second young was gone.

These downy young were estimated to be one to three days old. When the young was handled for measurements, it was turned over on its back; it struggled vigorously to regain its normal position but it did not give the slightest sound. It appeared very much afraid as it crouched in the hand, and it would not perch on one's finger.

Feeding Habits

We made numerous observations on the feeding habits of the Singing Quail in the cloud forest. In many cases the birds moved slowly and warily as they fed, but quickened their pace when they crossed a small clearing. The quail fed much in the manner of a domestic hen (*Gallus gallus*), by scratching first with one foot and then with the other, taking four or five strokes with each foot. The action is somewhat slower than that of a domestic hen and the length of each stroke a bit longer. We have never seen the method of obtaining food in which the bird makes a long sweeping stroke with one foot and then feeds in the debris (Warner and Harrell, 1957:128).

Normally the quail fed in the thick leaf litter of the forest floor, but it was not uncommon to see them feeding on moss-covered rocks and picking on moss-covered logs. As the birds continued to scratch for food, their bodies became half buried in the leaves. These depressions were conspicuous and enabled us to locate feeding areas when the quail were not singing.

Often, when a male found a large insect or other morsel, the female came quickly to take the particle from his bill. No note or call had been heard by us; yet the female had been, on occasions, feeding in another direction and must have been called by the male.

We examined the stomach and crop contents of two quail. One female, collected May 14, 1954, had 159 pokeweed seeds in the crop and 59 more in the stomach, an indication of the importance this seral newcomer to the forest may have in the food habits of this species. The animal remains in the crop consisted of five Coleoptera larvae (Elateridae), a pupa and an adult Lepidoptera, an adult Diptera, seven Hemiptera, and three spiders (Arachnida). The second bird, a male collected on May 17, 1953, by Paul S. Martin in the open pine–oak forests near La Joya de Salas, Tamaulipas, had nine

unidentifiable seeds, two larval Coleoptera (Elateridae), one adult Carabidae, one larva and one pupa Lepidoptera, and one Acarina in the crop. The animal matter in the stomachs of both birds was too finely macerated for specific identification, but it consisted of insect remains.

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GENERAL NOTES

Attraction of nocturnal migrants by lights on a television tower.—Allen (1880. *Bull. Nutt. Orn. Club*, 5:131–138) called attention to the fact that birds killed themselves by flying against the lights of lighthouses. Some of the lighthouses at which bird mortality occurred had red lights, others white, some had flashing, and some had fixed lights. Gastman (1886. *Amer. Nat.*, 20:981) estimated that a thousand birds (fall migrants) were killed at electric light towers in Decatur, Illinois.

More recently, Pough (1948. *Audubon Mag.*, 50:354–355) described mass mortality of migrants on the Empire State Building, New York, but made no mention of lights on the building. Howell, Laskey, and Tanner (1954. *Wilson Bull.*, 66:207–209) indicated that migrating birds may be attracted by the light beam of airport ceilometers.

Mortality of nocturnal migrants at television towers has also received attention, and presently several studies of this phenomenon are in progress.

In their outstanding analysis of bird mortality at a 950-foot television tower in Topeka, Kansas, Tordoff and Mengel (1956. *Univ. Kans. Mus. Nat. Hist. Publ.*, 10:17–20) discussed, among other things, the randomness of the sample of birds killed and calculated the number of migrants, assuming that the birds were uniformly spaced across the sky and neither attracted to the tower nor dispersed by it.

Recently the present writers made observations at a 984-foot television tower located 10 miles west of Champaign, Illinois, and obtained evidence that nocturnal migrants may be attracted by the red lights which are placed at 140-foot intervals along the tower.

During the night of May 29–30, 1957, there was a notable migration of birds in the vicinity of Champaign County. One or the other of the writers was present at the television tower from 8:00 p.m., May 29 until 5:15 a.m., May 30. The area was overcast and a light mist fell during part of the night. The surface wind was light from the E.S.E. Graber did not arrive at the tower until 11:30 p.m., but heard birds passing over the city of Champaign between 10:00 and 11:00 p.m. and also at two places along the 10-mile route from city to tower when he stopped to check on the migration. Upon reaching the transmitter he was immediately impressed by the great number of bird calls heard in the vicinity of the tower. It was apparent that there were more birds near the tower than away from it.

Besides hearing the birds we found that we could see birds passing the tower through the beam of an automobile spotlight. The spotlight beam reached the top of the tower, and we could judge the height of passing birds by the positions of the red tower lights and the attachment points of three sets of cable guys. Table 1 summarizes counts of birds which we made between 1:24 and 5:03 a.m.

Throughout this period migrants were around the tower and from call notes we identified Veeries (*Hylocichla fuscescens*), Dickcissels (*Spiza americana*), and Indigo Buntings (*Passerina cyanea*). Many of the birds probably were warblers, but we could not be certain of their identity.

The migrants were not evenly distributed but appeared in waves from the south. In the vicinity of the tower they were obviously confused, and their behavior was similar to that described for birds in a ceilometer beam by Howell, Laskey, and Tanner (1954. *Wilson Bull.*, 66:209). The migrants flew quickly through the framework of the tower, then circled at the edge of the lighted area and passed through the tower again. Most birds flew between elevations of 400 and 900 feet, but a few were above the tower and some were as low as 150 feet. In spite of the numerous obstructions which the framework of the tower offered and the fact that as many as 51 birds passed through or near

the tower in one minute, very few struck it. We heard several hit during the night but failed to find specimens the following morning. The number of birds heard to call per minute varied from 9 to 26, and the number seen per minute varied from 5 to 51 (Table 1). We could not tell how many times an individual bird was counted, for birds entered the beam and the tower structure from every possible direction.

The spotlight beam itself may have had some effect on the migrants, but certainly the birds behaved in the same confused manner whether the spotlight was on or off. When the spotlight was off we could see those migrants that passed very close to the red tower lights, and it was apparent that birds entered the lighted area from different directions. How long an individual bird may have flown about the tower we do not know, but from the call notes we felt certain that new birds were arriving regularly while others were moving away to the north or northwest.

TABLE 1
SUMMARY OF OBSERVATIONS MADE AT TELEVISION TOWER ON MAY 29, 1957, CHAMPAIGN COUNTY, ILLINOIS

Time CDST a.m.	Minutes	Bird notes heard	Birds heard per minute	Birds seen	Birds seen per minute	Elevation of most birds (feet)
1:24–1:32	8	70	9	78	10	600–900
1:55–2:00	5			106	21	400–600
2:04–2:09	5	104	21			
2:25–2:31	6			185	31	400–500
2:33–2:37	4	102	26			
2:40–2:44	4	102	26			
2:45–2:49	4			202	51	Under 500
3:03–3:05	2			33	17	
3:20–3:24	4	102	26			
3:25–3:30	5			155	31	400–600
3:50–3:54	4	101	25			
3:55–4:02	7			151	22	400–500
4:22–4:29	7	101	14			
4:30–4:40	10			101	10	400–500
4:50–4:56	6	51	9			
4:56–5:01	5			26	5	
5:03	Quite light but birds are still passing.					

With the spotlight we could track individual birds as they approached the tower, but usually lost them as they entered the tower framework. Three times we tracked individual birds away from the tower. Two of these flew to the west-northwest and one to the northeast, and all three gained altitude as they left the tower area. Several times we tracked birds as they left the tower framework and saw them circle and return to the tower.

Because the television transmitter itself was turned off (at 12:45 a.m.) before our observations began, we assumed that the confusion of migrants was caused solely by the lights.

Observations made between 3:30 a.m. and 5:45 a.m. on November 5, 1957 corroborated this view. At this time the sky was overcast, but there was no precipitation. When we arrived at the tower (approximately 3:30 a.m.) the transmitter was off, but the tower lights were on. We noticed a few birds fluttering about the outdoor lights of the transmitter building and identified five Slate-colored Juncos (*Junco hyemalis*) a Myrtle Warbler (*Dendroica coronata*), and a Swamp Sparrow (*Melospiza georgiana*). We heard other birds calling as they flew about the transmitter tower and counted eight call notes

per minute during a four-minute period. In quick succession, we then made call note counts of migrants as follows: one mile east of the tower at a place without lights—one bird heard in five minutes, two miles southeast of the tower—no birds heard in five minutes. Returning to the base of the tower, we continued making counts as follows: with tower lights on, 30 birds in four minutes; all lights off, no birds in four minutes; tower lights on, 9 birds heard, all near the end of a four-minute period; lights on, 7 birds in four minutes; lights on, 55 birds in four minutes; lights off, 6 birds heard, all in the first two minutes of a five-minute period; lights on, no birds in first two minutes, but after the lights had been on four minutes we heard 76 call notes in the next four minutes.

Turning off the tower lights definitely eliminated the congestion of migrants about the tower. Immediately after the lights went off, we could tell by the diminishing volume of call notes that birds were leaving the vicinity, and in less than two minutes all birds were out of hearing. After the tower was relighted it took from one to two minutes for the first birds to come into hearing, but thereafter the number of call notes increased dramatically.

We could not identify, with certainty, any of the migrants that we heard during the night, but at 7:15 a.m. we found five freshly killed birds (three Fox Sparrows, *Passerella iliaca*; one Golden-crowned Kinglet, *Regulus satrapa*; and one Woodcock, *Philohela minor*), and three crippled birds (two Slate-colored Juncos and one Golden-crowned Kinglet) under the east and west guys which support the tower.

Our observations indicate that confusion of nocturnal migrants by tower lights occurs only on nights when the ceiling is low, and migrants are apparently forced to fly near or below the 1000- to 3000-foot level. On clear nights or on nights when cloud cover is high, we learned, through the use of special audio equipment (unpublished manuscript) that numbers of high-flying migrants pass the vicinity of the tower without becoming confused.

Thus, calculations of total numbers of migrants based on the sample of birds killed at television towers are erroneous on at least two counts: (1) migrants are attracted to the towers by the tower lights, and (2) only a very small per cent of the birds which reach the tower are killed.—William W. Cochran, *WCIA, Champaign, Illinois, and* Richard R. Graber, *Illinois Natural History Survey, Urbana, Illinois, April 24, 1958.*

Early record for the Ivory-billed Woodpecker in Kentucky.—An early record from Kentucky seems to indicate a greater amount of wandering among Ivory-billed Woodpeckers (*Campephilus principalis*) than has commonly been attributed to them. Col. Wm. Fleming noted in his journal for March 7, 1780, while near St. Asaph's, or Logan's Fort, about 20 miles south-southeast of Harrodsburg, that he had met with a species of woodpecker new to him (N. D. Mereness, 1916. "Travels in the American colonies," pp. 632–633). He saw two individuals, "the Cock and the hen," the former having "a bright red head with remarkable large tuft of feathers on the Crown . . . the body and the wings White and black." One of the birds was shot, the female, Fleming thought (but probably a male of the previous year, according to Dr. James T. Tanner [letter to K. L. Dixon, June 25, 1958]). Fleming's description was essentially as follows: ". . . the feathers on the throat and belly and part of the wing and tail a shining black, it had nine stiff and strong feathers in the tail. . . , the middle one being six inches long from where the feathers begins. . . , its wings ten Inches long from the shoulder [*bend*?] to the tip, 18 long feathers in the wing, the two first and longest black[,] the 3rd tipd with white and each succeeding one more and more till the next to the back

are white, both above and below, the front and fore part of the Crown black, from the junction of the upper and lower bill white feathers on each side, leaving a triangle of black feathers from the Eyes and back part of the Crown which is deep red, . . . [.] its legs was an inch and a half long with four toes. . . , the two outer ones the longest and four inches in length[.] the bill white and bony verry strong and firm. . . , which is three inches in length, the tongue is six inches in length. The Iris when dead of a bright Yellow. . . , it weighed upwards of 1 lb."

Fleming evidently began counting primaries with the longest one, not with the outermost. Judging from Ridgway's measurements (1914. *U.S. Nat. Mus. Bull.* no. 50, pt. 6: 167, and pl. 8), the wing was larger than an Ivory-bill's, and the leg shorter, but it is not clear how the measurements were taken, and they may have been only approximate. The bill length is only slightly too large for *Campephilus*, and the total foot length seems right.

Tanner (1942. *Nat. Audubon Soc. Res. Rept.* 1) considered as the result of mistaken identity or, at least, unproved, the claims of Ridgway (*op. cit.*, p. 168), and of Allen (*in* Bent, 1939. *U.S. Nat. Mus. Bull.* no. 174:12) that this woodpecker formerly occurred in Franklin and Monroe counties, Indiana. Wetmore, however, recorded archeological evidence, presumably from the 15th or 16th centuries, of its occurrence in Scioto County, Ohio (1943. *Wilson Bull.*, 55:55). Although the present record does not validate the Indiana reports, it does make them appear more plausible.

Editorial help from K. L. Dixon and, through him, Dr. Tanner, is acknowledged with thanks.—DANIEL MCKINLEY, *Biology Department, Bowdoin College, Brunswick, Maine, August 7, 1958.*

Production of pellets by a Blue Jay.—A captive immature Blue Jay (*Cyanocitta cristata*), which was recovering from a broken wing, habitually perched in a "mimosa" tree in our yard at Greenbelt, Prince George's County, Maryland. Mr. C. V. Morton, U.S. National Museum, identified the tree as (*Abizzia lebbeck*).

As soon as we placed the jay in the tree it flew excitedly from branch to branch, gleaned insects from the leaves and branches, and ate the flowers of the tree. On two occasions, once on July 7, 1958, and once several days before, the bird regurgitated a hard pellet composed entirely of compressed blossoms of this tree. In each case, the pellet's surface was a hard, rough greenish-yellow crust. The interior was softer and consisted of the reddish tips of the flowers. The pellets were about half an inch in length and had two slightly tapering ends.—DONALD H. LAMORE, *605 College Street, Nevada, Missouri, August 26, 1958.*

Ruby-throated Hummingbird captured by a Praying Mantis.—A friend of mine, Conrad Steele of Lexington, Virginia, told me recently of a curious incident. Early in September, 1957, at Lexington, he saw a praying mantis (*Mantis* sp.) capture a hummingbird. While he is not particularly familiar with birds, the Ruby-throated Hummingbird (*Archilochus colubris*) is our only hummingbird. While sitting on a porch near which were some flowers that hummingbirds had been visiting, he detected a fluttering noise in a bush. Walking to the spot, he found that a mantis had its claws around a hummingbird's neck. When he clapped his hands the insect released the bird, which flew a short distance and fell to the ground. He picked the bird up, making sure that it was a hummingbird. After resting on his hand for a moment the bird buzzed away, apparently in good condition.—J. J. MURRAY, *109 East Broadway, Louisville 2, Kentucky, December 18, 1957.*

Black-throated Gray Warbler in Michigan.—On April 30, 1958, Dr. William R. Solomon, of the University of Michigan's University Hospital, reported seeing a male Black-throated Gray Warbler (*Dendroica nigrescens*) on the east side of Ann Arbor, Washtenaw County, Michigan. The morning of May 1, I went to the area where he had last seen the bird and soon found it in a small grove of medium-sized deciduous trees. The bird was active, moving often from tree to tree and rapidly searching the leaves of each tree for food. During the time I watched the bird it sang repeatedly and occasionally gave a low call note.

After watching the bird for about ten minutes, I collected it. The bird, an adult male (UMMZ No. 152892), was fat, weighing 11.0 grams. Its right testis measured 3×2 millimeters (left testis destroyed by shot). The stomach was full of small insect remains. The tail of the bird was undergoing an abnormal molt. The three outer rectrices of the left side and four inner rectrices of the right side were new feathers approximately four-fifths grown.

This appears to be the first record of the Black-throated Gray Warbler in Michigan. The occurrence of this western species in Michigan is not so surprising when one considers that it has been recorded in the East at least in Massachusetts, New York, Ohio, and Ontario, and is regularly seen in winter in Florida and Louisiana.—Norman L. Ford, *University of Michigan Museum of Zoology, Ann Arbor, Michigan, May 22, 1958.*

Rough-legged Hawk takes prey from Marsh Hawk.—On January 2, 1957, 12 miles southwest of Gibson City, Ford County, Illinois, I noticed two hawks seemingly engaged in a battle. Fifty yards above a corn field a dark-plumaged Rough-legged Hawk (*Buteo lagopus*) was pursuing a female or immature male Marsh Hawk (*Circus cyaneus*). Both birds displayed surprising flying ability, but neither appeared able to outmaneuver the other. After three minutes, the Marsh Hawk dropped a small, mouse-sized mammal which the Rough-leg swooped and caught 15 feet above the ground. After regaining an altitude of 75 feet the Rough-leg rapidly flew southwest with the prize in its talons, while the Marsh Hawk flew north and resumed hunting.—Robert P. Kirby, *University of Michigan Museum of Zoology, Ann Arbor, Michigan, June 10, 1958.*

WILSON ORNITHOLOGICAL SOCIETY NEWS

Members are reminded that the Fortieth Annual Meeting will be held at Rockland, Maine, June 11–14, 1959. The local committee has arranged an array of interesting field excursions which will be listed in a detailed announcement to be mailed shortly.

A Note from the Treasurer

Active and Sustaining Members received statements for dues two months early this year. This procedure was adopted in order to eliminate the added expense of sending the March issue of *The Wilson Bulletin* to those who would not be renewing their memberships. All delinquent members will be suspended before the mailing of the March, 1959, issue.

The treasurer hopes that members will respond to this first notice, and not make necessary the use of additional Society funds for the mailing of second notices. Please remember that postal rates for first class mail have increased 25 per cent.

The treasurer's address appears on the inside front cover in case you have mislaid your statement.

My term as editor has been the more pleasant for the firm support of the officers of the Society, and the prompt and generous aid of the members of the Editorial Advisory Board. William A. Lunk is singled out for special mention in view of his supervision of the processing of color plates. Other persons who contributed to the preparation of recent issues include Dean Amadon, James Bond, Jerram Brown, Allan Cruickshank, John Davis, W. B. Davis, J. J. Hickey, S. D. Ripley, G. W. Salt, P. B. Street, W. L. Thompson, and H. B. Tordoff. I wish to express my gratitude to these persons, and to Martha W. Dixon, who bore the brunt of preparation of the indexes.—K. L. D.

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

Books: List B-4

Important gaps among earlier works, in the holdings of the Josselyn Van Tyne Memorial Library, continue to be filled; and recent works are constantly being added. The following titles are of books added since publication of List B-3, in September, 1956 (*Wilson Bulletin*, 68:267–268).

Those wishing reprints of this and the earlier book lists should contact the Josselyn Van Tyne Memorial Library (Wilson Ornithological Society), Museum of Zoology, The University of Michigan, Ann Arbor, Michigan.

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THE ORNITHOLOGIST'S RESPONSIBILITY TO THE FUTURE

A Contribution from the Wilson Ornithological Society Conservation Committee

An effort to anticipate and prepare for the future seems desirable, because our generation bears a responsibility for passing on to the next a potential for continued well-being, particularly in the area of bird conservation. Any estimate of the future must be based on projections of past experience and cannot possibly be much more than an assessment of relative probabilities. Such estimates, however, provide the only reasonable basis for long-range planning and have become standard practice in the world of business and government. Inasmuch as we must attempt to ensure the protection of birds and the well-being of man, there appears to be little merit in a policy of deliberate conservatism in our estimate of the future.

The trend in growth of the human population constitutes the key element in long-range planning. Continued rapid growth of our population in the United States appears to be accepted generally by demographers. The possibility of acceptance of population control seems remote. The human birth rate tends to reflect the nation's economic status, and it is certain that government will do everything within its power to maintain prosperity. A major atomic war appears to be the only event which might check the current explosive trend in numbers of people in the foreseeable future.

Projections of the total United States population, based on high fertility and low mortality assumptions characteristic of the period since the end of World War II, have been estimated to be: 202,910,000 in 1965; 237,580,000 in 1975; 342,673,000 in 2000; and 501,825,000 in 2050 (Greville, 1957:27). Luck (1957:903) considered a population of 600 million by 2050 almost inevitable. In the event that these estimates seem excessive, we may be reminded that as recently as 1941 a study of recreational needs anticipated a population of only 158 million by about *1980* (U.S. Natl. Park Serv., 1941:5).

The demand for outdoor recreation promises to grow at a faster rate than the population. The amount of leisure available to the average person has been increasing steadily. The 5-day work week is almost universal, and vacations with pay are an established custom. Old-age insurance and pension plans provide for increasing retirement of the aged. Raushenbush (1955:92) predicted a 37.5-hour work week or its equivalent in annual working time by 1960 and a 35-hour week by 1965. Despite a shorter work week and a heavy tax burden, the trend in disposable income has been upward (Dewhurst and Assoc., 1955:90). The mobility of this population is increasing at a logarithmic or percentage rate. Automobile ownership is increasing more rapidly than population, and the movement of traffic is being facilitated by extension and improvement of the highway system. Clay *et al.* (1955:8–9) reported that almost 58 million motor vehicles were registered in 1954, one for "every 700 feet of every lane in both directions on all streets and highways in the Nation." They predicted that vehicle registrations would reach 81 million by 1965. Also, extensive use of inexpensive aircraft as a future mode of family transportation does not place excessive stress on the imagination.

That the public has been using its increased leisure, income, and mobility to utilize outdoor recreation is in abundant evidence. Statistics reveal that outdoor recreation has been increasing more rapidly than the population. The use of national parks almost doubled in the decade 1947–1956 (Clawson, 1958:23). The very rapid increase in the recreational use of national wildlife refuges is of particular significance to the ornithologist. Clawson (1958:49) showed that the recreational use of national wildlife refuges more than doubled from 1951 to 1956. He compared this "with an increase of 48 per cent for the national park system, and of 75 per cent for the national forests, in the same period." Clawson classified use of national wildlife refuges in 1956 as: hunting, 6 per cent; fishing, 37 per cent; and other, including picnicking, swimming, and wildlife observation, 57 per cent, and he observed that "It would be interesting to know how much of the use was solely or primarily for the . . ." purpose of wildlife observation. Interesting indeed. A survey in 1955 determined that 21 per cent of all people 12 years of age and older hunted, fished, or did both and expended approximately $2,850,979,000 in these activities (U.S. Fish and Wildlife Serv., 1956:7, 17). Outdoor recreation is big business and promises to get bigger.

Projections of the future use of national parks and forests for recreation have been attempted. From 53 million visits recorded in national forests in 1956, it is anticipated that an increase to 65 million in 1960 and to 360 million in 1980 may be expected; from 55 million visits in the national park system in 1956, it is estimated that 60 to 80 million visits may be anticipated in 1960 and 135 to 440 million visits in 1980 (Clawson and Held, 1957:342). This forecast of demand for recreation in the national forest and park systems probably reflects that which may be contemplated for private lands and state, county, and municipal facilities. Thus, we are in the somewhat strange business of struggling to increase facilities to accommodate a rapidly increasing horde seeking outdoor recreation and at the same time using every means within our power to encourage greater interest in Nature as a means of insuring support for its preservation and wise use.

Baker (1952:20) believes that "The greatest progress made in conservation in our generation has been growing recognition of its basic relation to human welfare . . ." There are more private and government agencies encouraging interest in outdoor recreation and the conservation of natural resources than ever before. The business world recognizes that it has a major stake in outdoor recreation. That these agencies together with the public are making their interests known with increasing power is evident in legislation of all kinds. The biologist has a responsibility here which will grow in

importance, the responsibility of guiding this power in a realistic direction. And, certainly, the biologist's role in the task of improving upon the perceptive capacity and proper conduct of the public in the out-of-doors will also take on increased importance. Pierce (1957:284) has pointed out some of the responsibilities which we bear as ornithologists.

The well-being of birds will be most vitally affected where the task of meeting the requirements of an exploding human population necessitates permanent change in habitat. The problem resolves itself into whether upwards of 220 million people can live in the continental United States without causing a major adjustment in bird populations. Birds, and people for that matter, must eventually come to terms with the limitations of their environment. An appraisal of this problem and the knowledge needed for its solution or understanding requires projection of trends in land and water use, especially as relates to change in habitat.

Of the total rural land area of the continental United States (1,903,706,000 acres), approximately 24 per cent is federally owned and federally administered. Of the federal lands, excluding Indian lands (which are not federally owned) and military reservations, it is believed that at least 95 per cent of the remaining 377 million acres will remain in federal ownership (Clawson and Held, 1957:3, 5). In a discussion of major changes in land use to 1975, Wooten and Anderson (1955:1) believed that "the total forest area may be maintained at about the present level. . ." Except for isolated problems, it seems likely that little change will take place on federal lands in the foreseeable future which would result in catastrophic adjustment of bird life. The most important considerations here will be an increasingly intensive forest management program, delay in acquisition of strategic lands to complete the national waterfowl refuge system, management of visitors to insure protection of the bird species in critical status, and excessive exploitation of nonrenewable resources.

The effect of intensive forest management on bird life should be kept under observation. Inasmuch as pines can be grown more quickly than hardwoods, it seems likely that they will be used to an increasing extent for meeting the timber needs of the future. The currently expanding application of herbicides from airplanes to relieve pines of competition from hardwoods has a great potential for producing permanent change in bird populations. Because pure stands of pine support but little wildlife, Lay (1958:5) considered that the problem resolved itself into saving a sufficient proportion of hardwoods to meet the needs of wildlife while removing enough to permit production of a satisfactory stand of pine.

Bellrose and Scott (1955:311) have pointed out the need for stepping up the acquisition of land to complete the national waterfowl refuge system. Competition for land is becoming increasingly severe. Land prices and conflict of interest may reach a point where purchase of land for wildlife refuges will become prohibitive. The encroachment of human activities on wetlands is evident in the remarks of Farley (1955:16): "Today and for years past we have watched marshes and ponds disappear as agriculture has expanded. In the black prairie-pothole region of western and southern Minnesota and eastern North and South Dakota, agricultural drainage removed, in each of the years 1949 and 1950, about 22,000 potholes, amounting to some 63,000 acres. These areas were the most productive waterfowl lands in the United States, fully equal to the best producing areas in Canada. Similar drainage is occurring in many coastal sections, which are most important to the birds as wintering grounds. Most of the great natural marshes of the Gulf are being ruined or seriously damaged for waterfowl use by salt-water intrusion as a result of the Intracoastal and connecting canals, and by exploration for

sulfur and oil. Waterfowl of the Pacific Flyway are rapidly approaching a crisis because the lush marshes which once supported myriads of birds wintering in California and northern Mexico are being turned into cotton and rice fields, orchards, and urban developments."

In 1934 it was estimated that the federal government should own and develop 7,500,000 acres of wetland for the protection of our waterfowl resource (Farley, 1955:17). In 1956, Shaw and Fredine (1956:32) reported that there were 3,270,000 acres in federal waterfowl refuges, thus leaving over 4,000,000 acres to be acquired. In addition, it was estimated that the states should acquire 5 million acres primarily for waterfowl. In 1956, Shaw and Fredine (1956:31) reported that "at least 1,500,000 acres in waterfowl areas are now administered by the States." Judged by present-day tempo, it does not seem likely that we can gamble with delay much longer in acquiring the additional lands. It is most encouraging to learn that the recent amendment to the Duck Stamp Act provides that, beginning July 1, 1960, virtually all receipts from the new $3 duck stamp will be used to acquire wetland areas needed to complete the refuge system. I am doubtful as to whether even this will provide for the necessary acceleration. Another 20 years and we may well be spending our effort trying to keep what we have rather than acquiring new lands. In addition to drainage for the purpose of increasing the area in cropland, such activities as waterway construction, drainage for mosquito control, industrial and urban expansion, highway construction, and disposal of human waste will compete for wetlands with increasing severity. Our concern with waterfowl refuges, great as it is, should not cause us to lose sight of the importance of the neighborhood marsh which provides a center of interest for bird watchers close to home.

Undoubtedly, the most marked adjustments to bird populations will take place on those lands used for agriculture, and by far the majority of our birds live on these lands. Wooten and Anderson (1957:32) estimated that "Roughly, three-fifths of the total area of land in the continental United States, or 1,158 million acres, is in farms, and two-fifths, or 746 million acres, is not in farms. Nearly half the land not in farms, or 353 million acres, is used for grazing. But much of this large area is publicly owned and is used jointly for other purposes, including forests, wild game preserves, watersheds to supply water for irrigation, power, and other uses." Land inventories indicate the following distribution of cropland and pasture on farms: cropland, 465 million acres; and grassland, pasture, and range, 633 million acres (Wooten and Anderson, 1957:33).

Higher crop yields must be achieved in the not too distant future if our population continues to increase at the present rate. Fortunately, the outstanding feature of modern agriculture has been the steady increase in productivity per acre. Leonard (1957:117), however, reported that "In spite of current food surpluses, there is concern in the United States about how to achieve food production that will be adequate to maintain the present diet for the anticipated population of 1975." Wooten and Anderson (1957:33) counseled that "If recent trends continue in the next 25 years, some 20 to 30 million acres of permanent grassland suitable for cultivation likely will be brought into the cropland–pasture rotation. In addition, possibly 10 million acres of fertile farm woodland and brushland likely will be cleared for cropland and rotation pasture, chiefly to improve the layout and add to the tillable acreages of existing farms in the farm-forest regions." The trend is toward larger areas in individual farms (Dewhurst and Assoc., 1955:809). Using the rate of production for 1953 as a base, Wooten and Anderson (1957:35) estimated that livestock products must be increased by more than 40 per cent and crop production by about 25 per cent by 1975. "The greatest increase needed in crop production would be in field crops, feed grains, hay, soybeans, and especially pasture. Crops

for which little or no increase in production would be needed to meet requirements include major food grains, potatoes, and cotton." (Wooten and Anderson, 1957:36).

The reduction of crop losses through more effective protection against insects and diseases will take on added importance as our need for food increases. More general use of chemicals for this purpose may be expected unless greater progress is made in the direction of biological control. Unless chemical poisons are found which are more specific for the problem at which aimed and less toxic to birds, losses may be expected and over greater areas than is the case today. The ornithologist bears a responsibility for adding to his knowledge of the long-range effect of modern insecticides on birds. He should at least be prepared to advise the entomologist and the public of probable consequences to bird life which may be expected from the use of particular insecticides in particular areas.

Cultivated fields undoubtedly support greater total numbers of birds now than they did prior to cultivation. Sharp reduction or elimination of waste in cultivated grains and weed plants, however, could result in food shortages for birds which could well become a major limiting factor. The intensive effort to obtain chemical control of weeds seems to be succeeding, and inefficient harvest methods are receiving increased attention. Waste grain from cultivated crops constitutes the greatest volume of food consumed by many birds. Losses in cleanly harvested crops of wheat, oats, barley and rye, even with the best combine adjustment, will vary from 1 to 4 per cent of the yield (Huber and White, 1953:4). It has been estimated that an amount equivalent to 10 per cent of the yield of corn remains in the fields as a result of inefficient harvesting methods (Bateman, Pickard, and Bowers, 1952:3). A marked reduction of waste in corn has already been achieved by a harvesting technique in which the corn is shelled in the field. Even if harvesting techniques did not improve, more corn will be gleaned by livestock in the future. As the demand for livestock production increases it seems likely that more green corn will be cut and chopped in the field to be fed as ensilage, thereby utilizing the whole corn plant.

Wildlife depredations in unharvested grain promise to become of progressively greater concern. Following a study of depredations on cultivated grains by waterfowl in southwestern Manitoba, Bossenmaier and Marshall (1958:31) recommended "The initiation of a long-range program for the development of feasible cultural methods of control . . ." This would seem to constitute an intelligent long-range objective wherever bird depredations constitute a threat.

It is apparent that our agricultural lands are particularly subject to change, and the majority of our birds live on these lands during all, or at least critical periods, of their lives. Our knowledge of the relationship of agricultural land use practices to bird populations is incomplete except for certain game birds and even here our knowledge can be improved upon. Without such knowledge we cannot forecast and prepare for likely changes in bird populations coming out of a more intensive agricultural program. Many changes on farm land are of a subtle nature from the standpoint of their effect on birds. While the trend is all in one direction, the amount of change in any one year is too small to attract much attention. During the past 10 years many miles of osage orange hedge have been bulldozed out in the midwestern United States. This must certainly have had a marked effect on the populations of those species regularly found nesting and rearing young in these hedges. Fencerows, ditchbanks, and roadsides grown to heavy herbaceous or woody cover have been "cleaned up" and many odd, unproductive bits of land have been cleared of brush or drained to improve efficiency of operations and to extend tillable lands. These activities undoubtedly have brought about changes

in bird populations which have gone unrecorded. Some species have lost out, others have been favored. But who really knows very much about the adjustment demands being made on continental bird populations as a result of the gradual change taking place on farm land.

An effort also needs to be made in the direction of evaluating agricultural practices which might prove advantageous to future farm needs and to birds. Wide-row corn seems to be one such practice (Vohs, 1958MS).

What the necessary increase in future livestock production may mean to birds also constitutes a problem. The development of improved pasture in the southeastern United States has resulted in marked changes in bird life. Attention, however, has been centered primarily on the local reduction of quail populations (Scott and Klimstra, 1954:6). The demand for grazing privileges on federal lands may well become a problem of increasing difficulty for administrators.

The importance of wildlife as a reservoir of diseases and parasites affecting livestock and man will certainly be cause for progressively greater concern as the human population and its need for food grows. Our knowledge in this field is so incomplete that intelligent action is impossible in many cases. A thoroughgoing knowledge of this subject is needed, if for no other reason than to insure against unwarranted wildlife control or eradication programs.

I have not seen estimates on the total area of land devoted to urban and industrial use or to highways, airports, rights-of-way, and other high value purposes. It is certain that the area devoted to such use will tend to parallel population growth. Wider dispersal of such key areas as a defense measure against atomic attack is being encouraged. The recently approved national highway program involves construction of a 41,000-mile network of interstate highways on an average 300-foot right-of-way which will place over 1 million acres of land along the pavement (Zuckel and Eddy, 1957:38). Egler (1958: 576) estimated that there are now 50 million acres of rights-of-way land. He (1958:573) defined rights-of-way land as "those narrow threads of land which serve for transportation and communication of man and materials. They include highways, railroads, electric power and telephone lines, and pipe lines for gas, oil, and coal." He pointed out that the rights-of-way of utility corporations comprised an acreage greater than all six of the New England states combined.

Management of these vast rights-of-way holdings should be investigated from the standpoint of effect on bird populations. It seems likely that lands devoted to such use will increase in area and, with increasingly intensive use of surrounding lands, may virtually constitute refuge areas for certain species of birds if properly managed. Egler (1958:574) wrote of the use of 2,4-D, 2,3,5-T, and ammonium sulfamate in the control of brush on rights-of-way land as follows: "It must be understood that these chemicals have no known adverse effects on any animals. If used unwisely, they do have an extremely detrimental effect on wildlife habitat, and this, in its way, is far more disastrous than any killing of the animals themselves." Egler (1958:577) also pointed out that "In most cases shrub communities retard reforestation more successfully than do grasslands."

Urban and suburban residential areas are expanding at a rapid rate. Perhaps the average family of the future will tend to satisfy more of its needs for pleasure in the out-of-doors and for escape from the pressures of civilization in its own back yard. The ornithologist should prepare to offer advice on neighborhood management of birds as a part of this scheme of things.

Zahniser (Callison, 1957:150–151) reported that according to available records in 1953

there were 2,030 state parks comprising 5,077,331 acres and a report for 1951 showed 17,142 county and city parks totaling 644,067 acres. Additional parks will undoubtedly be established, especially small parks in urban areas. However, it seems likely that the addition of parks will not parallel population growth. Such parks will receive increasing use and unless managed properly may serve more as a refuge for nuisance species of birds than desirable forms.

While the total water area will be very small by comparison to the land area, it can be of great strategic importance to birds. Impoundments for purposes of hydroelectric power will probably be installed wherever feasible, for they have the advantage of being based on a nonexhaustible source of energy. Impoundments for public water supplies and industry will probably tend to parallel population growth, and their location will reflect the dispersal of industry. The average daily quantity of water consumed "for all purposes increased from 600 gallons per capita in 1900 to 1,100 gallons in 1950 and 1,300 gallons in 1955. By 1975 the country will be using 1,800 gallons of water a day for every man, woman, and child" (U.S. Soil Conservation Serv., 1957:5). The added water areas will undoubtedly enhance the well-being of some birds, if they can be managed for multiple purposes. Water pollution is closely associated with the density of population and with industry; hence, unless protective measures are rigidly enforced, the aquatic foods, especially of animal origin, of birds may undergo undesirable alteration. Industrial pollution may cause direct loss as in the case at Lake Calumet, Illinois, where severe losses among migrating shore birds in fall have been traced to soluble lead.

A reliable basis for appraising long-range adjustments in the numbers and species of birds is needed. Perhaps a running inventory of bird populations, classified to land use or habitat category, in winter and during the breeding season would provide such an index. Excellent information is available for waterfowl, and our knowledge of upland game birds is good and is improving rapidly. The nesting season data published annually in *Audubon Field Notes* are helpful. Nevertheless, objective data of this nature are generally deficient for other species. Ornithologists are either underestimating the importance of this need, are shunning it as a personally unprofitable chore, or are living with the false hope that someone else will do it. The job needs doing in representative habitat categories throughout the country, and responsible leaders must take the initiative in filling the gaps in these censuses of birds. In Illinois, we were fortunate enough to have benefited from the foresight of Stephen A. Forbes who encouraged extensive, systematic censuses of birds throughout Illinois in 1906–09. The data obtained (Forbes and Gross, 1922, 1923) were classified by land-use category. These censuses are being repeated now, some 50 years later, as a means of interpreting the adjustments which have taken place.

Another matter of general concern is the need for early acquisition of land for wildlife management areas. Shepard (1957:9–10) has emphasized the need for "immediate action . . . to preserve specific areas of land before they are overrun and lost forever" and recommended that industry might do well to participate in the acquisition of such lands. He points out that even now "The preservation of even small bits of marshlands or woods representing the last stands of irreplaceable biotic communities is interwoven with the red tape of law, conflicting local interest, the overlapping jurisdiction of governmental and private conservation bodies, and an intricate tangle of economic and social considerations." Along these lines, it is my personal belief that wildlife conservation agencies are gambling with their future well-being when they concentrate all of their land purchasing resources in the so-called waste lands and fail to obtain small, evenly dispersed parcels of land throughout intensively cultivated areas.

Another matter which will attract special consideration will be an increasing demand for birds to hunt. A part of this demand will be met by commercial, controlled shooting areas where the hunter may buy pen-reared game birds for hunting. The search for exotic game birds to occupy those areas where game birds are absent or scarce is likely to receive greater emphasis.

This analysis constitutes an effort to examine problems of bird conservation in the light of human progress. Glass (1957:11) has observed that "Few biologists, outside of an occasional leisure thought, seem to think very frequently or deeply about human progress." While the material presented here barely outlines the problem, it is sincerely hoped that it will serve to stimulate ornithologists to make a careful, critical, and imaginative examination of what the future holds for bird conservation.

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ORNITHOLOGICAL LITERATURE

NOMINA AVIUM EUROPAEARUM. By Harriet I. Jørgensen. Copenhagen: Ejnar Munksgaard, 1958: $5\frac{1}{2} \times 8\frac{1}{4}$ in., 283 pp., 1 fig. 26 Danish Kron.

In 1941 Harriet I. Jørgensen of Denmark and Cecil Blackburne of England collaborated in a glossary of the names of the birds found regularly in western Europe as given in 17 of the languages of that region. The present volume, by Harriet I. Jørgensen as sole author, is a further contribution to the subject, with the material brought down to date in consonance with present-day usage, and arranged for easy consultation in a modern systematic classification instead of the former somewhat confusing alphabetic sequence. Two languages, Yugoslav and modern Greek, have been added since these are important in current ornithological literature, and the list has been made complete by the inclusion of 128 additional birds of rare or casual occurrence, so that 579 species now are covered. A further useful feature is the addition of a standard topographic chart of a bird in which 52 parts, of structure or plumage, are named in 20 languages (with Latin as the additional tongue). Anyone who has sought such terms in the usual foreign language dictionaries will appreciate the value of this information. Since names frequently vary in usage in England and in America, "North American" is added as a separate item throughout the book, wherever pertinent. A separate index for each language facilitates the location of any desired name.

In the present day when interest in ornithological studies is spread widely through the lands on both sides of the Atlantic this unique volume offers definitely useful service in identifying the terms under which birds are described in current literature of the various countries. It is thus a valuable addition to any ornithological library, useful to professional and amateur alike. In examining the book one must admire the knowledge of languages that it displays, as well as the meticulous care with which it has been prepared to insure correct expression in every detail.—ALEXANDER WETMORE

A FIELD GUIDE TO THE BIRDS OF PUERTO RICO. By James B. McCandless. I.A.U. Press, San Germán, P.R., 1958: $8\frac{1}{2} \times 5\frac{1}{2}$ in., viii + 68 pp., paper-bound, $2.00.

The author, a Mayaguez physician, calls this booklet, printed by offset, a supplement to Peterson's *Field Guide to the Birds*. Spanish names, abundance, seasonal occurrence and habitat are given for each of the 190 species discussed. The section on field marks is omitted from the accounts of the 137 species which also occur in the United States, and the reader is referred to Peterson's 1947 edition by page number. The 53 species not covered in Peterson are treated in detail.

Introductory pages contain information on bird finding areas, the seasons, what species may be expected in each type of habitat, and a chart showing dates of occurrence for regularly seen seasonal birds. Appendices include a list of extinct and extirpated species, a problematical list and a short bibliography. Both Spanish and English names are indexed.

The individual species accounts would have been strengthened by more complete comments on voice. Some species are covered; others not. The tourist would like to know, for example, that the familiar cardinal-like whistle is the song of the Puerto Rican bullfinch. Technically, the book contains such errors as wrong or misspelled scientific names and deviations from the current check-list order of arrangement.

These minor faults, however, in no manner detract from its purpose as simply a supplemental field guide and Baedecker for the Puerto Rican visitor.—PHILLIPS B. STREET

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Anderson, William S(herwood), 125 N. James St., Peekskill, New York 1957
†Annan, Ormsby, 270 Birch Street, Winnetka, Illinois 1956
Anthes, Clarence A(lvin), 707 N. Moreland Blvd., Waukesha, Wisconsin 1939
Anthony, Jesse D., 722 - 1st Ave., East, Grand Rapids, Minnesota 1944
*Arbib, Robert S(imeon), Jr., 807 Crystal Springs Rd., Hillsborough, California 1947
Armington, Sven, Blanchegatan 18, Stockholm, Sweden 1948
*Armstrong, Virginia, Old Concord Rd., South Lincoln, Massachusetts 1939
Arnett, John Hancock, Jr., Harrisburg State Hospital, Harrisburg, Pennsylvania 1944
Arnold, Elting, 4914 Dorset Ave., Chevy Chase 15, Maryland 1941
Arny, Samuel A., 6515 Willston Drive, Apt. 2, Falls Church, Virginia 1947
†Aronoff, Arthur Edward, 11 Fifth Ave., New York 3, New York 1948
Ashton, Randolph, 800 Crown St., Morrisville, Pennsylvania 1941
Atkeson, Thomas Zephaniah, P.O. Box 1643, Decatur, Alabama 1953
Austin, Mrs. Harold C., 1116 Mandana Rd., Oakland 10, California 1950
Austin, Oliver L(uther), Jr., Florida State Museum, Gainesville, Florida 1930
Axtell, Harold H., Buffalo Museum of Science, Humboldt Park, Buffalo 11, N. Y. 1950
Badger, Lester R., R.R. 1, Excelsior, Minnesota 1957
Baepler, Donald H(enry), Dept. of Zoology, University of Oklahoma, Norman, Okla. 1955
†Bagg, Aaron Moore, Farm St., Dover, Massachusetts 1948
Baier, Mrs. John, R.D. 3, 600 Vine Hill Way, Martinez, California 1949
Bailey, Alfred Marshall, Museum of Natural History, City Park, Denver 6, Colorado 1928
*Bailey, Harold H(arris), Rockbridge Alum Springs Biological Laboratory, Route 2, Goshen, Virginia 1908
Baillie, James Little, Royal Ontario Museum, Queens' Park at Bloor, Toronto 5, Ont. 1939
Baird, James, Norman Bird Sanctuary, Third Beach Road, Middletown, Rhode Island 1954

†Baker, Bernard W., R.D. 1, Judson Rd., Spring Lake, Michigan 1938
†Baker, John H(opkinson), 1130 Fifth Avenue, New York, New York 1930
Baker, Maurice F(rank), Wildlife Bldg. API, Auburn, Alabama 1947
*Baker, Paul S(eaman), 21 Woodlot Lane, Huntington, L.I., New York 1946
Baker, Rollin Harold, The Museum, Michigan State College, East Lansing, Michigan 1938
Baker, William C(alvin), 559 Euclid St., Salem, Ohio 1931
Baldwin, Mrs. Amy G., 6335 Kimbark Ave., Chicago 37, Illinois 1943
Baldwin, Paul H., Dept. of Zoology, Colorado State University, Fort Collins, Colorado 1956
*Ball, Kathleen E., 11719 - 133rd St., Edmonton, Alberta, Canada 1946
*Balsom, Mrs. Amos Parker, 2209 E. Stratford Court, Milwaukee 11, Wisconsin 1949
Banks, Clinton S(eeger), 202 Wilma Ave., Steubenville, Ohio 1945
Banta, Edna, Mary Gray Bird Sanctuary, Route 6, Connersville, Indiana 1945
*Barber, Mrs. Harold A., 23863 Fordson Dr., Dearborn, Michigan 1952
Barbour, Llewellyn P(helps), 4780 Wood St., Willoughby, Ohio 1948
Bard, Fred George, Museum of Natural History, Regina, Saskatchewan, Canada 1946
*Barrett, Edward V., 1315 W. 79th St., Chicago 20, Illinois 1958
†Bartel, Karl E(mil) Edgar, 2528 W. Collins St., Blue Island, Illinois 1934
Barth, R. H., Jr., Biological Laboratories, Harvard University, Cambridge 38, Mass. 1957
Bartleson, Fred D(urant), Jr., 3815 McGregory Blvd., Ft. Myers, Florida 1952
*Bartlett, Guy, 1053 Parkwood Blvd., Schenectady 8, New York 1938
Bartlett, L(awrence) M(atthews), Dept. of Zoology, University of Massachusetts, Amherst, Massachusetts 1957
Bartlett, Wesley H., 122 South Ridgley, Algona, Iowa 1936
*Bartsch, Paul, "Lebanon," Gunston Hall Rd., Lorton, Virginia 1894
Bastin, Eric W(alter), 43 Inglewood Dr., Apt. 2, Hamilton, Ontario, Canada 1951
*Batchelder, Edgar M(arden), 56 Orchard St., Marblehead, Massachusetts 1941
†Batts, H(enry) Lewis, Jr., 1211 Knollwood Avenue, Kalamazoo, Michigan 1946
*Baxter, William, Jr., Route 2, Middletown, Delaware 1945
Baylor, L(eslie) M(ilton), 1302 S. Fourth Ave., Pocatello, Idaho 1954
Beals, Everett K(err), 1310 N. 11th St., Manhattan, Kansas 1953
Beardslee, Clark Smith, 132 McKinley Ave., Kenmore 17, New York 1942
Beardsley, M(argaret) Hortense, 330 N. Chestnut St., Ravenna, Ohio 1941
Bebb, Forrest, 1300 Boston Ave., Muskogee, Oklahoma 1955
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Becker, Ezra, New Albin, Iowa 1957
Beddall, Mrs. Barbara G(ould), 2502 Bronson Road, Fairfield, Connecticut 1958
Beecher, Mrs. Barbara J., 330 Elm St., Bennington, Vermont 1956
Beecher, William J(ohn), Chicago Natural History Museum, Chicago 5, Illinois 1948
Beer, James R(obert), Dept. of Entomology and Econ. Zoology, University of Minnesota, St. Paul 1, Minnesota 1957
Behle, William H(arroun), Dept. of Biology, University of Utah, Salt Lake City 1, Utah 1935
Behrens, Harry Carl, Box 1055, Rapid City, South Dakota 1950
*Belcher, Paul Eugene, 230 Mineola Ave., Akron 13, Ohio 1938
Bell, Henry, III, U.S. Geol. Surv., Agric. Research Center, Beltsville, Maryland 1946
Bell, Miriam, Toledo State Hospital, Toledo 3, Ohio 1958
Bellrose, Frank, Jr., Illinois Natural History Survey, Havana, Illinois 1935
*Bender, R. O., Coble's Mill Rd., Bridgeton, New Jersey 1957
Benne, Bart L., 338 N. Van Brunt, Kansas City, Missouri 1956
Bennett, A. F., 701 W. Main Street, Denison, Texas 1955
Bennett, Esther V(orena), 704 W. Mill, Carbondale, Illinois 1954
Bennett, Holly Reed, 2457 Orchard St., Chicago 14, Illinois 1949
Benson, Seth, 645 Coventry Rd., Berkeley 7, California 1930
Bent, Mrs. M. V., 275 Monroe Ave., Rochester, New York 1955
Benton, Allen H(aydon), Dept. of Biology, New York State College for Teachers, Albany, New York 1953
†Berger, Andrew J(ohn), Dept. of Anatomy, University of Michigan, Ann Arbor, Mich. 1940
Berger, Daniel D(avid), 510 E. MacArthur Rd., Milwaukee 17, Wisconsin 1953
†Bergstrom, E(dward) Alexander, 37 Old Brook Rd., West Hartford 7, Connecticut 1943
*Berkowitz, Albert Clarence, 1912 Grand Ave., Des Moines 14, Iowa 1946
Betts, Amelia J(eanette), Baldwin City, Kansas 1953

Biaggi, Virgilio, Jr., College of Agriculture, Mayaguez, Puerto Rico 1945
Bibbee, P. C., Concord College, Athens, West Virginia 1958
*Binder, Kay, 3838 W. 61st Street, Chicago 29, Illinois 1958
Binford, L(aurie) C(harles), 330 Grove St., Glencoe, Illinois 1954
Birch, Robert Lee, Dept. of Biology, West Virginia University, Morgantown, W. Va. 1950
Birkeland, Henry, Roland, Iowa 1934
Birkenholz, Dale E(ugene), Dept. of Biology, University of Florida, Gainesville, Fla. 1957
Black, Charles T(heodore), Route 1, Box 480, East Lansing, Michigan 1935
†Blain, Alexander W(illis), 2201 Jefferson Ave., East, Detroit 7, Michigan 1902
Blake, Charles H(enry), P.O. Box 613, Hillsboro, North Carolina 1950
Blake, Mrs. Henry S., 1933 Westwood Drive, Topeka, Kansas 1950
Blanchard, Harold H(ooper), 32 Calumet Rd., Winchester, Massachusetts 1946
Blanchet, Helen, 1406 Southfield Rd., Lincoln Park, Michigan 1954
Blaney, John L., Box 169 - 30 Tac. Recon. Sp. APO 123 c/o Postmaster, New York, N. Y. 1958
†Bleitz, Donald Lewis, 1001 N. McCadden Place, Los Angeles 38, California 1948
Bliese, John C(arl) W(illiam), Nebraska State Teachers College, Kearney, Neb. 1951
Bock, Walter J(oseph), Biological Laboratories, Harvard University, Cambridge, Massachusetts 1953
Bodsworth, Fred, 294 Beech Ave., Toronto 8, Ontario, Canada 1956
†Bond, James, 1900 Race St., Philadelphia 3, Pennsylvania 1945
Bond, Richard M(arshall), Kings Hill, St. Croix, U.S. Virgin Islands 1936
Bond, Richard R(andolph), Dept. of Biology, Salem College, Salem, West Virginia 1955
†Booth, Mrs. Robert V. D., 1085 Bank Street, Painesville, Ohio 1949
Bordley, James, III, 13 Main St., Cooperstown, New York 1957
Borell, Adrey Edwin, Soil Conservation Service, 321 New Custom House, Denver 2, Colorado 1936
*Borror, Donald J(oyce), Dept. of Zoology, Ohio State University, Columbus 10, Ohio 1927
Boughner, W. C., Apt. 9, 66 E. Cliff St., Somerville, New Jersey 1956
Bourdo, Eric Albert, Jr., Ford Forestry Center, L'Anse, Michigan 1951
Bowdish, Beecher S(coville), 16 Van Horn St., Demarest, New Jersey 1921
Bower, Mrs. F. L., RFD 1, Lee's Hill Road, Basking Ridge, New Jersey 1954
Boyd, Elizabeth M(argaret), Mount Holyoke College, South Hadley, Massachusetts 1941
Boyd, Ivan L., Dept. of Biology, Baker University, Baldwin, Kansas 1951
Boyer, George Frederick, Canadian Wildlife Service, c/o Southern Research Station, R.R. 2, Maple, Ontario, Canada 1949
Boyer, G(ertrude) Paula, 420 E. 2nd Ave., Roselle, New Jersey 1953
*Brackbill, Hervey G(roff), 2620 Poplar Dr., Baltimore 7, Maryland 1942
*Bradburn, Donald Muir, 461 Pine St., New Orleans 18, Louisiana 1950
Braden, Paula Lou, 1526 New York Ave., Brooklyn 10, New York 1953
*Branch, Mrs. Margaret G(amble), 1324 Wells St., Ann Arbor, Michigan 1952
Brandt, John Henry, Tr. Terr. of Pacific Islands, Truk, E. Carolina Islands (via Guam) 1958
Branum, Florence P(auline), 117 N. Ewing Street, Lancaster, Ohio 1946
Brauner, Joseph, 3855 Potomac Ave., Los Angeles 8, California 1942
Braunschweig, Mrs. Lee W(elsh), 712 E. Montgomery Ave., North Wales, Penn. 1953
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Brecht, Grace Elizabeth, 1328 Clinton Ave., Irvington 11, New Jersey 1949
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Breiding, George H(erbert), Naturalist, Oglebay Institute, Wheeling, West Virginia 1942
Brewer, Richard Dean, Dept. of Zoology, Vivarium Bldg., University of Illinois, Champaign, Illinois 1949
*Brigham, Edward M(orris), Jr., Kingham Memorial Museum, Battle Creek, Mich. 1931
Brigham, Edward M(orris), III, 621 E. Marengo, Flint 5, Michigan 1950
Bristow, Harry Sherman, Jr., 210 Washington Ave., Cedars-Wilmington, Delaware 1942
Broadbooks, Harold E(ugene), Southern Illinois University, Alton Residence Center, Alton, Illinois 1948
Brodkorb, Pierce, Dept. of Biology, University of Florida, Gainesville, Florida 1951
Brody, Gerald L(ee), University Hospital, Ann Arbor, Michigan 1954
Broley, Charles L(avelle), Delta, Ontario, Canada 1946

Bronoel, Joel, 2010 E. First St., Duluth 12, Minnesota 1957
Brook, Mrs. Margaret, 126 51st St., Des Moines 12, Iowa 1958
†Brooks, Maurice Graham, Div. of Forestry, West Virginia Univ., Morgantown, W. Va. 1927
Broun, Maurice, Route 2, Kempton, Pennsylvania 1935
Brown, Jerram L., Museum of Vert. Zool., Life Science Bldg., Berkeley 4, California 1950
†Brown, Laurence A(llyn), Jr., 434 Marlborough St., Boston 15, Massachusetts 1958
Brown, N(orman) Rae, Faculty of Forestry, University of New Brunswick, Fredericton, New Brunswick, Canada 1945
*Brown, Woodward H(art), 4815 Ingersoll Ave., Des Moines 12, Iowa 1949
Bruce, James A(ddison), 565 E. Spring St., Wooster, Ohio 1952
*Brueggemann, Anna L(ouise), 584 Sheridan Ave., Columbus 9, Ohio 1943
†Bruns, James Henry, 1820 Jefferson Ave., New Orleans, Louisiana 1941
Bryan, Burton Donald, 162 French St., Fall River, Massachusetts 1949
*Bryens, Oscar McKinley, Route 1, White Pigeon, Michigan 1924
Buchanan, Forest Wendell, Amsterdam, Ohio 1939
Buchheister, Carl W., 1130 Fifth Ave., New York 28, New York 1943
Buckland, George H(enry) E(dward), Box 343, Route 1, Batavia, New York 1949
Buckley, P(aul) A(nthony), 6024 Fieldston, Riverdale 71, New York, New York 1958
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*Bucy, Paul T(homas), R.D. 1, Box 278-A, Nitro, West Virginia 1957
Bull, John L., Jr., 1148 Virginia St., Far Rockaway, New York 1952
Bunnell, John R., 3867 Edgewood Ave., Ft. Myers, Florida 1953
Bures, Joseph August, Route 1, West Newton, Pennsylvania 1946
Burner, Florence H(elen), 5350 Reisterstown Rd., Baltimore 15, Maryland 1948
Burnham, Gladys L(ou), Dept. of Biology, Clarendon Junior College, Clarendon, Texas 1954
Burns, Robert David, Dept. of Zoology, University of Oklahoma, Norman, Oklahoma 1948
Burr, Irving W(ingate), 1141 Glenway, West Lafayette, Indiana 1945
Burt, William Henry, Museum of Zoology, University of Michigan, Ann Arbor, Mich. 1928
Burton, Donald E(rnest), 171 Strathearn Road, Toronto 10, Ontario, Canada 1953
Burtt, Benjamin P., 109 Haffenden Rd., Syracuse 10, New York 1956
Burtt, Harold E., 2163 N. Starr Ave., Columbus 12, Ohio 1953
Bushman, John, University of Utah, Dugway, Utah 1951
Butsch, Robert Stearns, Exhibit Museum, University of Michigan, Ann Arbor, Mich. 1947
Byers, Mrs. Esther, 2905 San Rafael, Tampa, Florida 1951
Cade, Tom, 3353 S. Lucile Lane, Lafayette, California 1950
Cagle, Fred R., Dept. of Zoology, University of Tulane, New Orleans 15, Louisiana 1942
Cahalane, Victor H(arrison), 80 Fernbank Ave., Delmar, New York 1933
Calef, Robert, 821 Granger Ave., Ann Arbor, Michigan 1954
Calvert, Earl Wellington, R.R. 2, County Home, Lindsay, Ontario, Canada 1937
Calvin, Robert L(eal), R.D. 3, Pulaski Rd., New Castle, Pennsylvania 1951
Camp, Mrs. Dorothy I(rene), R.D. 1, Stuart Lake, Marshall, Michigan 1957
Campbell, Louis W(alter), 4531 Walker Ave., Toledo 12, Ohio 1926
*Campbell, Mildred F(lorence), 29 N. Hawthorne Lane, Indianapolis 19, Indiana 1938
*Cannon, Mrs. Gail C(lark), 38 Liberty Place, Rockaway, New Jersey 1958
Cansfield, William Buck, Clean Lake School Camp, Dowling, Michigan 1958
Cardinoli, Mrs. Lillian E., Jolian Farm, R.D. 2, Box 460, Jamesburg, New Jersey 1958
Carl, Harry G., 2304 Davie St., Davenport, Iowa 1949
†Carnes, Mrs. Herbert E., 31 Dogwood Lane, Tenafly, New Jersey 1944
Carpenter, Charles C., Dept. of Zoology, University of Oklahoma, Norman, Oklahoma 1951
Carpenter, Floyd S., 2402 Longest Ave., Louisville 4, Kentucky 1934
Carroll, Robert P., 213 Maiden Lane, Lexington, Virginia 1942
†Carrothers, Vera, 14704 Alder Ave., East Cleveland 12, Ohio 1938
Carson, L(enwood) B(allard), 1306 Lincoln St., Topeka, Kansas 1948
Carter, Charles E(dward), 1339 - 30th Street, Orlando, Florida 1958
Carter, Dennis L(ee), 408 S. Prairie Ave., Fairmont, Minnesota 1947
*Carter, Mrs. E. W., Route 2, Perrysburg, Ohio 1946
†Cartwright, Bertram William, c/o Ducks Unlimited (Canada), 201 Bank of Commerce Bldg., Winnipeg, Manitoba, Canada 1930
Cassel, J(oseph) Frank(lin), Dept. of Zoology, North Dakota Agricultural College, Fargo, North Dakota 1940

Cater, Milan B(rison), P.O. Box 15, Clifton Forge, Virginia 1944
†Chalif, Edward Louis, 37 Barnsdale Rd., Short Hills, New Jersey 1947
Chamberlin, B(arnwell) Rhett, Route 1, Box 30, Matthews, North Carolina 1957
*Chamberlaine, Lee B., 145 Dorwin Ave., Syracuse 5, New York 1957
*Chambers, W(illie) Lee, Route 1, Box 410, Robinson Road, Topanga, California 1909
Chaniot, George E., Jr., 1069 W. Prairie, Decatur, Illinois 1956
Chapelle, Francis O(berlin), U.S. Army Hospital, West Point, New York 1954
Chapin, James P(aul), American Museum of Natural History, Central Park W. at 79th St., New York 24, New York 1945
Chapman, Blanche Hammond, 1325 S. 19th St., Birmingham, Alabama 1953
Chapman, Floyd B(arton), 392 Walhalla Rd., Columbus 2, Ohio 1932
*Chapman, Herman Floraine, 712 South Dakota Ave., Sioux Falls, South Dakota 1947
Chapman, Lawrence B., R.F.D., Box 90, Hubbardston, Massachusetts 1940
*Chell, Thomas Ross, 1220 Beck Lane, Lafayette, Indiana 1952
Choate, Ernest A., 411 Rodman Ave., Jenkintown, Pennsylvania 1954
Chutter, Mildred C., Box 229, Athens, Ohio 1936
Clark, Mrs. Ben P., 2736 Hilltop Circle, Gadsden, Alabama 1952
Clark, George A(lfred), Jr., Osborn Zool. Laboratories, Yale University, New Haven, Connecticut 1955
†Clarkson, Mrs. Edwin O., Wing Haven, 248 Ridgewood Ave., Charlotte 7, N. C. 1940
Clement, Roland C(harles), 26 Brookfield Rd., Riverside 15, Rhode Island 1941
†Clements, H(iram) Everest, 49 Stoneham Rd., Rochester 10, New York 1949
*Clise, Mrs. Charles Frances, 1030 - 39th Ave., North, Seattle 2, Washington 1957
*Clow, Marion, Box 163, Lake Forest, Illinois 1929
Clyde, Mrs. Brooke, 201 Laurel St., San Francisco 18, California 1958
Cobb, Boughton, 25 East End Ave., New York, New York 1949
†Coffey, Ben Barry, Jr., 672 N. Belvedere, Memphis 7, Tennessee 1927
Coffey, Mrs. Lula C(ooper), 672 North Belvedere, Memphis 7, Tennessee 1952
Coggeshall, Robert D., Billington Rd., East Aurora, New York 1956
Cogswell, Howard L(yman), Dept. of Biological Sciences, Mills College, Oakland 13, California 1944
Cole, Mrs. Richard D., 625 Valley Lane, Towson 4, Maryland 1955
*Cole, Mrs. Whiteford R., Jr., 1746 Sulgrave Rd., Louisville 5, Kentucky 1956
Collier, Gerald, 3634 Muscatel Ave., Rosemaid, California 1956
Collins, Henry H., Jr., 1200 Post Road, Scarsdale, New York 1952
Compton, L. E. & Mrs., R.D. 1, Box 21, Waukesha, Wisconsin 1957
Compton, Lawrence Verlyn, Biological Division, Soil Conservation Service, Washington 25, D. C. 1923
†Conboy, Mrs. John William, 417 Studebaker St., Mishawaka, Indiana 1954
Condit, Anna R(uckman), 3235 Clay Street, Apt. 5, Denver 11, Colorado 1958
Conkey, John H., 11 Chestnut St., Ware, Massachusetts 1947
Conn, Robert Carland, 755 Ross Lane, Bound Brook, New Jersey 1945
Connell, Ernest D(ouglas), St. Andrews, New Brunswick, Canada 1958
Conrad, Charles L(ouis), 137 N. 11th St., Wheeling, West Virginia 1937
Cook, Fannye A(dine), Apt. 4 B, 827 N. State St., Jackson, Mississippi 1923
Coombes, Robert Armitage Hamilton, The Zoological Museum, Tring, Hertfordshire, England 1936
*Cooper, Kenneth K(ing), 5430 Netherland Ave., Bronx 71, New York 1958
Cope, James B(ronwill), Earlham College, Richmond, Indiana 1949
Corbett, Kenneth B., R.D. 1, Box 68, Lancaster, Pennsylvania 1957
Cors, Paul B(eaumont), 722 Woodside Ave., Ripon, Wisconsin 1952
*Cottam, Clarence, Welder Wildlife Foundation, P.O. Box 1396, Sinton, Texas 1929
Cottrell, George William, Jr., 70 Lake View Ave., Cambridge 38, Massachusetts 1941
Cottrille, W(illiam) Powell, 6075 Brown's Lake, Jackson, Michigan 1949
Cottrille, Mrs. W. Powell, 6075 Brown's Lake, Jackson, Michigan 1950
Cox, George W., Vivarium Bldg., Wright & Healy Sts., Champaign, Illinois 1954
Coy, Roy E., St. Joseph Museum, St. Joseph, Missouri 1953
*Crawford, Alan, Jr., White Horse Rd., Devon, Pennsylvania 1949
*Creager, Joe C(lyde), L. A. Cann Road, Drawer 1267, Ponca City, Oklahoma 1947
Crichton, Vincent, Chapleau, Ontario, Canada 1948
Crockett, David B., 3933 Kirkland Court, Route 3, Bloomfield Hills, Michigan 1955

Croft, Joseph E., 2366 Gladstone Ave., Louisville 5, Kentucky 1956
°Crofts, Robert J., 468 Thurston St., Toledo 5, Ohio 1957
Crowell, John B., Jr., 535 Jefferson Ave., Elizabeth 4, New Jersey 1952
Crowley, Lawrence D., 1212 Cascade, Boulder, Colorado 1955
Cruickshank, Allan Dudley, R.D. No. 1, Box 1590, Rockledge, Florida 1939
Cullen, Peter, 5115 Graceland, Indianapolis 8, Indiana 1956
Cumming, Fairman Preston, 824 Sutton Hill Rd., Nashville 4, Tennessee 1950
Cummings, G(eorge) Clark, 61 Broadway, New York 6, N. Y. 1952
Cunningham, James W., 3009 E. 19th Terrace, Kansas City, Missouri 1935
Cunningham, Richard L(ynn), 72 N.W. 33rd Ave., Miami 35, Florida 1953
°Currie, Mrs. Neill Alexander, Jr., 1104 Brook St., Fayetteville, North Carolina 1958
Curtis, Mrs. Vee K(aelin), 2412 Cohasset Rd., Chico, California 1950
Cuthbert, Nicholas L., Biology Dept., Central Michigan College, Mt. Pleasant, Michigan 1950
Dana, Edward Fox, 57 Exchange St., Portland 3, Maine 1939
Dane, Benjamin, Dept. of Zoology, Cornell University, Ithaca, New York 1957
°D'Angelo R(alph), 32 Hamilton Ave., Hasbrouck Heights, New Jersey 1949
Darby, Richard T(horn), Prospect St., Sherborn, Massachusetts 1948
°Darden, Mrs. Colgate W(hitehead), Jr., University of Virginia, Charlottesville, Va. 1943
°Dater, Eleanor E., 259 Grove St., Ramsey, New Jersey 1949
Davant, Mary, 861 N. McLean Blvd., Memphis 7, Tennessee 1952
Davey, Winthrop N(ewbury), University Hospital, Ann Arbor, Michigan 1941
°Davidson, Mrs. W. F., 332 Summit Ave., St. Paul 2, Minnesota 1953
Davidson, William Mark, 1504 Bodell Street, Orlando, Florida 1933
Davis, Clifford Vernon, Dept. of Zoology and Entomology, Montana State College, Bozeman, Montana 1945
Davis, David E(dward), School of Hygiene and Public Health, Johns Hopkins University, Baltimore 5, Maryland 1940
Davis, John, Hastings Natural History Reservation, Carmel Valley, California 1939
Davis, L(ouie) Irby, Box 988, Harlingen, Texas 1933
Davis, Paul A(nthony), 829 Grant St., Gary, Indiana 1953
Davis, Russell S., Clayton, Illinois 1947
Davis, Wayne Harry, Dept. of Entomology and Econ. Zool., University of Minnesota, St. Paul, Minnesota 1953
†Davis, W(illiam) B., Dept. of Wildlife Management, College Station, Texas 1938
Davis, William Franklin, 1800 E. 105th St., Cleveland 6, Ohio 1947
Davis, W. Marvin, Faculty Exchange, University of Oklahoma, Norman, Oklahoma 1956
Davy, Roger H(ewson), P. O. Box 455, Guymon, Oklahoma 1957
Dawn, Walter H(enry), 176 Wentworth St., Charleston, South Carolina 1945
Dear, L(ionel) S(extus), P. O. Box 146, Port Arthur, Ontario, Canada 1939
Dechen, Mrs. Lillian Orvetta, 14 Summer St., Port Dickinson, via Binghamton, New York 1939
Deevey, Edward S(mith), Jr., Osborn Zoological Laboratory, Yale University, New Haven 11, Connecticut 1948
DeGarmo, William Russell, Kents Hill, Maine 1946
DeGroot, Dudley Sargent, Athletic Branch, S.A.D., USAREUR, APO 245, c/o Postmaster, New York, New York 1948
Dehner, Eugene W(illiam), St. Benedict's College, Atchison, Kansas 1944
Deininger, Leo A., 2583 E. 130th St., Shaker Heights 20, Ohio 1956
†Delacour, Jean Theodore, Los Angeles County Museum, Exposition Park, Los Angeles 7, California 1944
°Dempster, Rulon T., 1027 Edgmont Ave., Chester, Pennsylvania 1958
Denham, Reginald F(rancis), 100 Central Park, South, New York 19, New York 1948
Denton, J(ames) Fred, 1510 Pendleton Rd., Augusta, Georgia 1935
°De Schauensee, Rodolphe Meyer, Devon, Pennsylvania 1945
†Desmond, Thomas C(harles), Box 670, Newburgh, New York 1942
Devlin, Joseph M(ark), 218 S. 43rd St., Philadelphia 4, Pennsylvania 1953
Devitt, Otto Edmund, 83 Harding Blvd., Richmond Hill, Ontario, Canada 1935
Dexter, Ralph W., Dept. of Biology, Kent State University, Kent, Ohio 1958
°Dick, John Henry, Dixie Plantation, Meggett, South Carolina 1949

Dickerman, Robert W(illiam), Museum of Natural History, University of Minnesota, Minneapolis, Minnesota 1955
*Dickerson, Mrs. Stanley S., 222 DeVoe Ave., Spotswood, New Jersey 1956
Dickinson, J(oshua) C(lifton), Jr., Dept. of Biology, University of Florida, Gainesville, Florida 1939
Dilger, William C., Laboratory of Ornithology, Cornell University, Ithaca, N.Y. 1957
*Dingle, Edward von Siebold, Huger, South Carolina 1921
Dixon, J(ames) B(enjamin), 2266 Cranston Drive, Escondido, California 1936
Dixon, Keith Lee, Hastings Natural History Reservation, Carmel Valley, California 1946
Doan, Mrs. Blanche Evans, Apt. 13, 1228 S. 29th St., Birmingham 5, Alabama 1947
†Doering, Hubert R., 242 East Walton Place, Chicago 11, Illinois 1945
Dogger, James R., Dept. of Entomology, North Dakota Agricultural College, Fargo, North Dakota 1954
Domm, Lincoln V(alentine), Dept. of Anatomy, Stritch School of Medicine, Loyola University, 706 S. Wolcott Ave., Chicago 12, Illinois 1936
Donald, Mary F(rances), 6918 Belmont Lane, Milwaukee 11, Wisconsin 1951
Donegan, Marie, 920 E. Ann St., Ann Arbor, Michigan 1953
*Dorsey, George A., Darlington School, Rome, Georgia 1956
*Douglass, Donald W., Game Division, Michigan Dept. of Conservation, Lansing 26, Michigan 1929
Dowling, Paul Bruce, Route 1, Wentzville, Missouri 1950
Down, Edward H., 28 Lynton Mead, Totteridge, London N 20, England 1956
*Dressel, Evan C., 1177 E. Western Reserve Rd., Poland, Ohio 1956
Dresser, Mrs. James, Jr., 9620 Von Thaden St., Wichita, Kansas 1951
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Drum, Margaret, 217 South St., Owatonna, Minnesota 1937
†Drury, William H(olland), Jr., Drumlin Farm, South Lincoln, Massachusetts 1951
Duebbert, H(arold) F(ranklin), 152 N. 4th St., Oakes, North Dakota 1957
Duffield, Mrs. John W., 1472 Eskridge Way, Olympia, Washington 1948
Duffy, J(ohn) J(oseph), Jr., 428 E. 70th St., Kansas City 10, Missouri 1950
†Dugan, William Dunbar, 221 Pierce Ave., Hamburg, N. Y. 1945
DuMont, Philip A(tkinson), 4114 Fessenden St., N.W., Washington 16, D.C. 1928
*Duncan, Robert, 1151 Fulton Avenue, San Antonio 1, Texas 1956
Dundas, Lester Harvey, Horicon Wildlife Refuge, R.D. No. 2, Mayville, Wisconsin 1943
Dunn, Lawrence E., R.F.D., Gate, Oklahoma 1956
*Dunning, John Stewart, Granby, Connecticut 1951
Dunstan, Girvin Raleigh, 5030 Huron River Dr., Route 1, Dexter, Michigan 1950
Dusi, Julian L(uigi), Dept. of Zoology & Entomology, Alabama Polytechnic Institute, Auburn, Alabama 1941
†Duval, Allan J., Patuxent Research Refuge, Laurel, Maryland 1958
Dvorak, J. L., 6125 Eddy St., Chicago 34, Illinois 1958
Dyer, William A., 402 John St., Union City, Michigan 1947
Dzubin, Alex, 317 Field Husbandry Bldg., University of Saskatchewan, Saskatoon, Saskatchewan, Canada 1956
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Eaton, Stephen W(oodman), Dept. of Biological Sciences, St. Bonaventure University, St. Bonaventure, New York 1942
Eckelberry, Don R(ichard), 4 Foster Lane, Babylon, L.I., New York 1948
Eddy, Garrett, 4515 Ruffner St., Seattle 99, Washington 1947
†Edeburn, Ralph M(ilton), Dept. of Zoology, Marshall College, Huntington, West Virginia 1947
Edge, Mrs. Charles N(oel), 1215 Fifth Ave., New York 29, New York 1931
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*Edwards, K(enneth) F(rederick), 169 Hillendale Ave., Kingston, Ontario, Canada 1953
Edwards, R(oger) York, Parks Branch, Dept. Recreation and Conservation, Victoria British Columbia, Canada 1948
Egerton, Frank N(icholas), III, 1517 Caswell Place, Durham, North Carolina 1952
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Krug, Howard H(enry), Chesley, Ontario, Canada 1944
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Kuitert, Louis Cornelius, Agricultural Experiment Station, University of Florida, Gainesville, Florida 1938
Kunkle, Donald E., Box 121, Port Norris, New Jersey 1956
Labisky, Ronald F., Sect. of Wildlife Research, Nat. Hist. Surv., Natural Resources Bldg., Urbana, Illinois 1956
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Lacey, Mifton H., Box 614, Canton, Ohio 1939

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Land, Hugh Colman, Zoology Dept., University of Oklahoma, Norman, Oklahoma 1950
Landing, James E., 509 E. 10th St., Michigan City, Indiana 1956
Lanyon, Wesley E(dwin), American Museum of Natural History, New York, N.Y. 1955
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Lawrence, Mrs. Louise de Kiriline, The Loghouse, Pimisi Bay, Rutherglen, Ontario, Canada 1946
Lawson, Ralph, 5 Carpenter St., Salem, Massachusetts 1951
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Leavitt, Benjamin Burton, Dept. of Biology, University of Florida, Gainesville, Florida 1947
Leberman, Robert C(harles), R.D. No. 1, Saeger Hill, Meadville, Pennsylvania 1958
Leedy, Daniel L(oney), U.S. Fish and Wildlife Service, Branch of Wildlife Research, Washington 25, D. C. 1936
Lees-Smith, D(erer) T(hayer), Broadmeer Hospital, Crowthorne, Berkshire, England 1958
LeFebvre, Mrs. Joyce, 3889 Bellaire Ave., White Bear Lake 10, Minnesota 1953
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LeSassier, Mrs. John W., 1611 W. Indiana, Midland, Texas 1957
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Lewis, Mary E(velyn), 925 Dauphine St., New Orleans 16, Louisiana 1957
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Lewis, William O(wen), Box 22, Ivy, Virginia 1953
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Longley, William H(oward), P.O. Box 362, Kasson, Minnesota 1943
Longwell, John R(aymond), Maryland Dept. of Research and Education, Box 1510, Annapolis, Maryland 1958
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Manville, Richard H(yde), Fish and Wildlife Service, U.S. National Museum, Washington 25, D. C. 1941
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Meacham, Frank B., State Museum, Raleigh, North Carolina 1945
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Meanley, Brooke, Patuxent Research Refuge, Laurel, Maryland 1950
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Mellinger, E(nos) O(ren), Savannah N. W. Refuge, Box 4008, Port Wentworth, Georgia 1939
†Melone, Theodore G(ardner), Geology Library, Pillsbury Hall, University of Minnesota, Minneapolis 14, Minnesota 1947
Meltvedt, Burton W., Paullina, Iowa 1930
†Meng, Karl, State Teachers College, New Paltz, New York 1943
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*Mengel, Robert M(orrow), Museum of Natural History, University of Kansas, Lawrence, Kansas 1937
*Menninger, Phil B., 1724 Collins Ave., Topeka, Kansas 1949
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Meyer, Henry, Wisconsin State College, Whitewater, Wisconsin 1939
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Michaud, Howard H(enry), 824 Chauncey St., West Lafayette, Indiana 1938
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Mitchell, Robert W(etsel), 320 Iowa Street, Beaumont, Texas 1955
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Morgan, Allen H., 155 Newbury St., Boston 16, Massachusetts 1958
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Morrison, Kenneth Douglas, Mountain Lake Sanctuary, Lake Wales, Florida 1937
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Mueller, Helmut Charles, Dept. of Zoology, Birge Hall, University of Wisconsin, Madison 6, Wisconsin 1949
Muhlbach, W(alt) L(auritz), 2127 Ashby Ave., Berkeley 5, California 1951
Mumford, Russell E(ugene), Dept. of Forestry and Conservation, Purdue University, West Lafayette, Indiana 1949
Murie, Adolph, Moose, Wyoming 1932
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Myers, Richard F., Stevens Hall, University of Missouri, Columbia, Missouri 1952
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Nero, Robert William, Saskatchewan Museum of Natural History, Regina, Saskatchewan, Canada 1947
Nessle, James P., R.F.D. 1, Waterville, Ohio 1936
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*Nicholson, Donald John, Tuxedo, North Carolina 1945
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Norman, Edward d'Aubigny, 181 Stage Harbor Rd., Chatham, Massachusetts 1951
Norman, James L(ee), 2617 Elgin, Muskogee, Oklahoma 1948
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Northrop, Myron, 9304 Sylvan Hills Rd., North Little Rock, Arkansas 1945
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Nye, Frederick F., Jr., P.O. Box 451, McAllen, Texas 1943
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O'Callaghan, Terence C., Maromala R.D., Bay of Islands, Northland, New Zealand 1954
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Ogilvie, Phillip W., Museum of Natural History, University of Kansas, Lawrence, Kansas 1956
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Olson, Mrs. Monrad J., Box 595, Watford City, North Dakota 1946
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Randall, Robert Neal, 928 - 16th St., Bismarck, North Dakota 1939
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Rea, Gene, 251 Leland Ave., Columbus 2, Ohio 1948
Rea, Mrs. R. V., 856 Forest Ave., South Bend 16, Indiana 1958
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Reed, S(tuart) Arthur, 2780 E. Grand River Ave., East Lansing, Michigan 1957
Rees, Earl Douglas, 1504 N. Main St., Findlay, Ohio 1946
Reese, C(arl) R(ichard), 266 E. Dunedin Rd., Columbus 14, Ohio 1948
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Reese, Leonard E., 3016 Delta River Dr., Lansing 6, Michigan 1957
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Reichert, Elsa, Mirakel Repair Company, 14 W. First St., Mt. Vernon, New York 1950
Reilly, E(dgar) M(ilton), Jr., Box 21, Old Chatham, New York 1946
Renfrew, Mrs. Malcolm M., 104 Saratoga Rd., Buffalo 26, New York 1956
Rett, Egmont Z(achary), Museum of Natural History, Santa Barbara, California 1940
Reynard, George B., 105 Midway, Riverton, New Jersey 1950
Reynolds, William Pius, 1330 Foulkrod St., Philadelphia 24, Pennsylvania 1948
Rice, Dale W(arren), Box 1, U. S. Naval Station, c/o Navy 3080, F.P.O., San Francisco, California 1946
Rice, Orville O(wen), 1663 W. 28th St. Terrace, Topeka, Kansas 1953
Rich, Mrs. Eva, 150 W. 80th St., New York 24, New York 1952
Richards, Tudor, Dublin, New Hampshire 1951
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Richter, Carl H., 703 Main St., Oconto, Wisconsin 1947
Richter, G(eorge) William, 231 E. Main St., Canfield, Ohio 1954
Ricker, W(illiam) E(dwin), Pacific Biological Station, Naniamo, British Columbia, Canada 1943
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Riggs, Carl D(aniel), Dept. of Zoology, University of Oklahoma, Norman, Oklahoma 1943
Riggs, Jennie, 2005 Capers Ave., Nashville 5, Tennessee 1952
Rimsky-Korsakoff, V(ladimir) N(icholas), 220 Middle Rd., Sayville, L. I., N. Y. 1951
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Rising, Gerald R(ichard), 72 Allen's Creek Rd., Rochester 18, New York 1953
Rising, James D., 4406 Sunrise Dr., Kansas City, Missouri 1956
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†Robbins, Eleanor C(ooley), Patuxent Research Refuge, Laurel, Maryland 1936
†Robbins, Mrs. Chandler, II, Eastern Point, Gloucester, Massachusetts 1958
Roberts, Harold D., 818 Clark St., Stevens Point, Wisconsin 1946
Robertson, Mary J., R.D. 2, Box 83C, Homestead, Florida 1954
Robins, C(harles) Richard, Virginia Key, Miami 49, Florida 1949
Robinson, Peter J., 333 Crossman St., Jamestown, New York 1956
Robinson, Thane S., Western Michigan University, Kalamazoo, Michigan 1952
Roesler, Mrs. Carol S., June Road, Cos Cob, Connecticut 1949
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Rogan, Mrs. Francis E., 44108 Second St., East, Lancaster, California 1953
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Rogers, Gerald T., 643 N. Beachview Dr., Fort Walton Beach, Florida 1956
Rogers, John P., Wildlife Bldg., University of Missouri, Columbia, Missouri 1956
Rogers, K(ay) T(rowbridge), Dept. of Zoology, Oberlin College, Oberlin, Ohio 1952
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Romaine, Mrs. Lawrence B., Weathercock House, Middleboro, Massachusetts 1958
Rooney, James P., 1514 S. 12th Ave., Yakima, Washington 1947
†Root, Oscar M(itchell), Brooks School, North Andover, Massachusetts 1940
Root, Richard Bruce, Dept. of Zoology, University of California, Berkeley 4, Calif. 1953
Rorimer, Mrs. J. M., 6910 Point of Rocks Rd., Sarasota, Florida 1938
Rosche, Richard Carl, Dept. of Zoology, University of Kansas, Lawrence, Kansas 1953
Rose, W(illiam) C(umming), 710 W. Florida Ave., Urbana, Illinois 1949
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Ross, Hollis T., 29 S. 2nd St., Lewisburg, Pennsylvania 1956
Ross, James B., Reinhold Book Division, 430 Park Ave., New York 22, New York 1949
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Ruder, Clara Louise, 520 Franklin St., Wausau, Wisconsin 1954
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Russell, Stephen M(ims), 267 East Valley, Abingdon, Virginia 1952
Rustad, Orwin A., 1486 Fulham St., St. Paul 8, Minnesota 1957
Rutter, Russell James, Box 794, Huntsville, Ontario, Canada 1950
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Sadler, Doug(las) C(ampbell), R.D. 2, Ida, Ontario, Canada 1958
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Sanborn, Alvah W., Pleasant Valley Sanctuary, Lenox, Massachusetts 1951
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Sather, John Henry, Western Illinois State College, Macomb, Illinois 1956
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Satterly, J(ack), 15 Aldbury Gardens, Toronto 12, Ontario, Canada 1947
Sauer, Gordon C(henoweth), 425 E. 63rd St., Kansas City 10, Missouri 1949
Saugstad, N(els) Stanley, Route 4, Minot, North Dakota 1939
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Saunders, George B(radford), Box 131, Gainesville, Florida 1926
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Schaffner, Art(hur), 170 Laurel St., Buffalo 8, New York 1957
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Schnell, Jay H(eist), 1696 Paper Mill Rd., Meadowbrook, Pennsylvania 1953
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†Schultz, Albert B(igelow), Jr., Penryn Park, Port Hope, Ontario, Canada 1954
Schumm, William George, 302 C. St., LaPorte, Indiana 1944
Schwartz, Charles Walsh, 131 Forest Hill, Jefferson City, Missouri 1950
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Schwilling, Marvin D., Box 62, Pleasanton, Kansas 1951
Sciple, George W., 5715 Doolittle, Houston 21, Texas 1951
Scotland, Minnie B(rink), 42 Continental Ave., Cohoes, New York 1938
Scott, D. M., Dept. of Zoology, University of Western Ontario, London, Ontario, Can. 1950

Scott, Frederic R(obert), 115 Kennondale Lane, Richmond 26, Virginia 1947
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Scott, W(alter) E(dwin), 1721 Hickory Dr., Madison 5, Wisconsin 1938
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Seeber, Edward L(incoln), 493 Norwood Ave., Buffalo 22, New York 1944
Seibert, Henri C., Ohio University, Athens, Ohio 1941
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Shaver, Jesse M(ilton), 1706 Linden Ave., Nashville 12, Tennessee 1922
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Shetler, Stanwyn G(erald), Dept. of Botany, Cornell University, Ithaca, New York 1949
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Short, Wayne, 1130 Fifth Ave., New York 28, New York 1941
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Sibley, Charles G(ald), Fernow Hall, Cornell University, Ithaca, New York 1942
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Sieh, James G(erald), Biology Building, Okoboji, Iowa 1948
*Simmons, Mrs. Amelia C., 2676 N. Lake Drive, Milwaukee 11, Wisconsin 1943
†Simmons, Edward McIlhenny, Avery Island, Louisiana 1942
†Simmons, Grant Gilbert, Jr., Lake Ave., Greenwich, Connecticut 1949
Simon, Stephen Wistar, 402 Sharp St., Ashland, Ohio 1947
Singleton, Albert Ronald, 3968 Marburg Ave., Cincinnati 9, Ohio 1948
Skelton, Mrs. Kathleen Green, Middleton, Delaware 1949
Skutch, Alexander F(rank), San Isidro del General, Costa Rica, C. A. 1944
Slack, Mabel, 1004 Everett Ave., Louisville 4, Kentucky 1934
Smart, Robert W(illiam), New Hampton School, New Hampton, New Hampshire 1957
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Smith, Earl R(oy), Box 5271, New Orleans, Louisiana 1957
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Smith, Harry M(adison), 1602 State St., Columbus, Indiana 1936
Smith, Marion L(ucille), 429 S. Willard St., Burlington, Vermont 1949
Smith, Robert L(eo), Division of Forestry, West Virginia University, Morgantown, West Virginia 1945
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Smith, Thomas Price, 4320 Lawn Ave., Western Springs, Illinois 1951
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Snead, Mrs. Idalene F., 845 S. 42nd St., Birmingham 6, Alabama 1956
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Snyder, Dana Paul, Dept. of Zoology, University of Massachusetts, Amherst, Mass. 1949
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Snyder, L(ester) L(ynne), Royal Ontario Museum of Zoology, Queen's Park at Bloor St., Toronto 5, Ontario, Canada 1929
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Sooter, Clarence Andrew, U.S. Public Health Service, P.O. Box 625, Greeley, Colo. 1940
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Southern, William, 614 Prairie St., Clare, Michigan 1954
Spangler, Iva M., 128 E. Foster Parkway, Fort Wayne, Indiana 1939
Sparkes, Vera E., 2417 Lyndale Ave., N., Minneapolis 11, Minnesota 1951
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†Speirs, J(ohn) Murray, "Cobble Hill," R.D. No. 2, Pickering, Ontario, Canada 1931
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Sperry, John A., Jr., 1006 College St., Canton, Missouri 1957
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Stabler, Robert M(iller), Colorado College, Colorado Springs, Colorado 1939
Staebler, Arthur E(ugene), Biology Department, Fresno State College, Fresno, California 1937
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Stallcup, William B., Biology Dept., Southern Methodist University, Dallas, Texas 1951
Stamm, D(onald) D(aniel), P.O. Box 61, Montgomery, Alabama 1958
Stamm, Mrs. Frederick W., 2118 Lakeside Dr., Louisville 5, Kentucky 1947
Stanley, Eliot H., 1009 NE 17th St., Oklahoma City, Oklahoma 1955
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Starkey, G(ordon) Rankin, 201 Bobwhite Drive, Kerrville, Texas 1957
Starling, Alfred Arthur, 34 Pinnacle Rd., Rochester 20, New York 1958
Starr, Robert R., 700 Leslie Ave., Glasgow, Kentucky 1956
Starrett, William C(harles), Illinois State Natural History Survey, R.R. No. 2, Havana, Illinois 1933
Stasz, C(larence) E(mil), 179 Edgewood Ave., Audubon 6, New Jersey 1953
Stauffer, Ralph Stanley, 170 W. Washington St., Hagerstown, Maryland 1949
Stearns, Edwin I(ra), Jr., 601 Lake Ave., Wilmette, Illinois 1945
Stefanski, Raymond, Armstrong Creek, Wisconsin 1957
Stein, Robert C., Dept. of Biology, Ursinus College, Collegeville, Pennsylvania 1951
Steirly, Charles C., Waverly, Virginia 1958
Steitz, Alfred, Jr., 3829 E. 54th St., Tulsa 5, Oklahoma 1957
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Stevens, Charles E(lmo), Jr., 615 Preston Place, Charlottesville, Virginia 1947
Stevens, John R(heinhardt), Dept. of Life Science, Los Angeles City College, 855 N. Vermont Ave., Los Angeles 29, California 1958
Stevens, O. A., State College Station, Fargo, North Dakota 1926
Stevenson, Henry M(iller), Dept. of Zoology, Florida State University, Tallahassee, Florida 1943
Stevenson, James O(sborne), Fish and Wildlife Service, Dept. of the Interior, Washington 25, D. C. 1933
Steward, Orville M(ilton), P.O. Box 19, Fordham Road Station, Bronx 58, N.Y. 1950
Stewart, James R(ush), Jr., 844 Natchez, Shreveport, Louisiana 1954
*Stewart, Mildred, 2579 Queenston Rd., Cleveland 18, Ohio 1949
Stewart, Paul A(lva), Dept. of Conservation, 311 W. Washington St., Indianapolis 9, Indiana 1925
*Stewart, Robert Earl, Patuxent Research Refuge, Laurel, Maryland 1939
Stillwell, Jerry E., 408 Laurel Rd., Athens, Texas 1935
*Stine, Perna M., c/o Mrs. Chester Scherer, R.R. No. 6, Olney, Illinois 1931
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†Stokes, Allen W., Dept. of Wildlife Management, Utah State Agricultural College, Logan, Utah 1950
Stone, Walter D., Detroit Zoological Park, 8450 W. 10 Mile Rd., Royal Oak, Mich. 1957
†Stoner, Mrs. Dayton, 389 State St., Albany 6, New York 1945
Stoner, Emerson A(ustin), 285 East L St., Benicia, California 1947

Stophlet, John J(ermain), 2612 Maplewood Ave., Toledo 10, Ohio 1934
Storer, Robert Winthrop, Museum of Zoology, University of Michigan, Ann Arbor, Michigan 1938
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Stringham, Emerson, Box 986, Kerrville, Texas 1940
•Strong, R. M., 5716 Stony Island Ave., Chicago 37, Illinois Founder
Stull, W(illiam) D(eMott), R.F.D. No. 1, Delaware, Ohio 1952
Stupart, Barbara, 48 Russell Hill Rd., Toronto, Ontario, Canada 1952
Stupka, Arthur, R.D. No. 1, Gatlinburg, Tennessee 1935
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Sturges, Franklin W., Southern Oregon College, Ashland, Oregon 1955
Summers, Lawrence, Dept. of Chemistry, University of North Dakota, Grand Forks, North Dakota 1956
Sundell, Robert A(rnold), 94 Main St., Frewsburg, New York 1951
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Suthers, Roderick A(tkins), 129 Griswold St., Delaware, Ohio 1954
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Swanson, James D(ean), Route 2, Hartford, South Dakota 1958
Swedenborg, Ernie D(avid), 4905 Vincent Ave., S., Minneapolis 10, Minnesota 1929
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Swinebroad, Jeff, Dept. of Botany and Zoology, Douglas College, Rutgers University, New Brunswick, New Jersey 1953
Swingle, Mrs. Robert F(ranklin), P.O. Box 594, Aiken, South Carolina 1958
Swisher, John F., Jr., 336 South Main, Brigham City, Utah 1957
Sywalski, Robert J., 852 Joseph Ave., Rochester 21, New York 1956
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Tabler, Mrs. William B., 6 Glen Hill Rd., Louisville 7, Kentucky 1947
Tabor, Ava Rogers, 305 Canal Blvd., Thibodaux, Louisiana 1940
Tallman, William S(weet), Jr., 4 Linden Place, Sewickley, Pennsylvania 1940
Talvila, Elmer, 1 Faukland Rd., Scarborough, Ontario, Canada 1954
Tanger, John Carroll, Jr., 518 Carlisle St., Hanover, Pennsylvania 1954
Tanghe, Leo J(oseph), 852 Stone Rd., Rochester 16, New York 1943
Tanner, James Taylor, Dept. of Zoology, University of Tennessee, Knoxville 16, Tennessee 1937
Tashian, Richard E(arl), 1133 E. Catherine St., Ann Arbor, Michigan 1949
†Taylor, Arthur Chandler, 309 N. Drew St., Appleton, Wisconsin 1929
Taylor, R(obert) L(incoln), Inverness Drive, Flintridge, Pasadena 3, California 1947
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Teale, Edwin Way, 93 Park Ave., Baldwin, L. I., New York 1948
Terres, John K(enneth), Apt. 3D, 345 E. 57th St., New York 22, New York 1955
Terrill, Lewis McIver, Ulverton, R.D. No. 1, Melbourne, Quebec, Canada 1948
Thomas, Edward S(inclair), Columbus 14, Ohio 1921
Thomas, Jack Ward, P.O. Box 1042, Sonora, Texas 1957
Thomas, Landon B(aillie), 1006 Blaine St., Edgerton, Wisconsin 1947
Thomas, Mrs. Rowland, 410 E. Green St., Morrillton, Arkansas 1937
Thompson, Daniel Q., Ripon College, Ripon, Wisconsin 1945
Thompson, E. G., 586 Gulf Bldg. Extension, Houston 2, Texas 1957
Thompson, Katrina, 2039 Milford, Houston 6, Texas 1957
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Thompson, Max C., Museum of Natural History, University of Kansas, Lawrence, Kansas 1956
Thompson, William Lay, Museum of Vertebrate Zoology, University of California, Berkeley 4, California 1952
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Throne, Alvin L., University of Wisconsin–Milwaukee, Milwaukee 11, Wisconsin 1949
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Todd, W(alter) E(dmond) Clyde, Carnegie Museum, Pittsburgh 13, Pennsylvania 1911
Tomer, John S(haffer), 4045 E. 27th St., Tulsa, Oklahoma 1954

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Tomlinson, Roy E(ugene), 407 College Ave., Columbia, Missouri 1958
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Townes, George F(ranklin), Masonic Temple, Greenville, South Carolina 1953
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Townsend, Mrs. Frank, 333 Sunset Rd., Pompton Plains, New Jersey 1958
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†Tucker, Mrs. Carll, Penwood, Mount Kisco, New York 1928
Tucker, James M(itchell), Paoli, Indiana 1953
Turner, Robert H(arold), Mounted Route 1, Lime City Rd., Perrysville, Ohio 1953
Tutton, Terry T., Palmyra, Wisconsin 1956
Twomey, Arthur C(ornelius), Carnegie Museum, Pittsburgh 13, Pennsylvania 1936
Tyrrell, W. Bryant, 246 Park Ave., Takoma Park 12, Maryland 1947
Uhler, Francis Morey, Patuxent Research Refuge, Laurel, Maryland 1931
Ulrich, Mrs. Edward C., 193 LaSalle Ave., Buffalo 14, New York 1952
Ulrich, Edward C., 193 LaSalle Ave., Buffalo 14, New York 1952
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Urban, Emil K., Dept. of Zoology, University of Wisconsin, Madison 6, Wisconsin 1956
Ussher, Richard Davy, R.R. No. 1, Morpeth, Ontario, Canada 1947
Vaiden, M(eredith) G(ordon), Rosedale, Mississippi 1937
Valentine, Allen E., 28444 Parkwood, Inkster, Michigan 1957
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Van Cleve, G(eorge) Bernard, 323 S. Fairmount St., Pittsburgh 32, Pennsylvania 1954
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Van Deusen, Hobart M(erritt), 12 S. Mountain Ave., Apt. 37, Montclair, N.J. 1941
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Van Tets, G(errard) F(rederick), Dept. of Zoology, University of British Columbia, Vancouver, British Columbia, Canada 1955
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Wagner, Esther E., 22 Golden Hill, Bethel, Connecticut 1958
Wagner, Helmuth O., Ubersee Museum, Bremen, Germany 1945
Walker, Charles F(rederic), Museum of Zoology, University of Michigan, Ann Arbor, Michigan 1939
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Wallace, George J(ohn), Michigan State College, East Lansing, Michigan 1937
Wallace, Roy, 63 DuPont St., Toronto 5, Ontario, Canada 1952
Walsh, David Alfred, Box 653, Nome, Alaska 1958
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Wangensteen, Mrs. Owen H., 2832 River Road West, Minneapolis 6, Minnesota 1949
Ward, Gertrude L(uckhardt), Earlham College, Richmond, Indiana 1953
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Warter, Stuart L., Museum of Zoology, Louisiana State University, Baton Rouge 3, Louisiana 1956
Warters, Mary Ellen, 5115 Woodland Ave., Des Moines 12, Iowa 1950
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Watson, Robert J(ames), Box 75, Blacksburg, Virginia 1943
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Weise, Charles M(artin), Dept. of Zoology, University of Wisconsin, Milwaukee 11, Wisconsin 1949
Weller, Milton Webster, Dept of Zoology and Entomology, Iowa State College, Ames, Iowa 1950
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